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THE POPULATION ECOLOGY OF THE DAMSELFLY LESTES DISJUNCTUS DISJUNCTUS (ZYGOPTERA: ODONATA) IN THE ST. MARYS RIVER, MICHIGAN

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THE POPULATION ECOLOGY OF THE DAMSELFLY _LESTES_ _DISJUNCTUS_ _DISJUNCTUS_ (ZYGOPTERA:ODONATA) IN THE ST. MARYS RIVER, MICHIGAN

By

Walter Gilbert Duffy

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

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ABSTRACT

THE POPULATION ECOLOGY OF THE DAMSELFLY *LESTES DISJUNCTUS DISJUNCTUS* (ZYGOPTERA:ODONATA) IN THE ST. MARYS RIVER, MICHIGAN

By

Walter Gilbert Duffy

A demographic investigation of a natural population of *Lestes disjunctus disjunctus* inhabiting the St. Marys River, Michigan was conducted during 1982 and 1983. Field studies investigated life history, distribution, and demographics. Laboratory studies examined the influence of water temperature on egg development, the influence of water temperature, prey density, and coexisting predators on growth and survival of nymphs and the influence of fish on survival and habitat selection.

The 1982 cohort oviposited an estimated 3,202,000 eggs in the 4.03 ha study area. Mortality in the egg stage was estimated to be 77.2%. Egg mortality factors were: habitat loss through anthropogenic sources (18.9%), overwintering (16.7%), hatching difficulty (6.0%), and unexplained sources (35.6%). Relative mortality among 10 nymphal instars varied and was greatest in the final instar (71.4%). Relative mortality through all nymphal stages was 94.7%. An estimated 35,800 adults emerged from the study area yielding an estimated survival rate from the egg to adult stage of 1.2%. Lower potential fecundity in 1983 (45.2 eggs·♀$^{-1}$) than in 1982 (73.5 eggs·♀$^{-1}$) combined with increased

mortality in 1983 to produce a negative population rate of increase (λ) value of -0.612.

Growth of nymphs in the laboratory was significantly greater at 20.0°C than at 16.0°C. Differences in growth among prey density treatments were not significant. However, prey density did significantly influence survival of nymphs while water temperature did not.

Survival of nymphs in the laboratory was significantly lower in the presence of nymphs of the dragonfly Aeshna canadensis than in the presence of other coexisting predators. Other predators may also influence survival, although differences were not significant. Growth of nymphs was not influenced by coexisting predators.

In the absence of bluegill sunfish (Lepomis macrochirus) nymphs exhibited little discrimination among three cover densities or three cover types (macrophytes, aquarium bottom, and sides). In the presence of fish, nymphs selected or were restricted in distribution to macrophytes at all cover densities. Distribution of nymphs was significantly affected and survival reduced by bluegill.

ACKNOWLEDGMENTS

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Dr. Ted R. Batterson graciously provided limnological data from the study area. Paul E. Roettger drafted the figure illustrating macrophyte distribution. John R. Craig, George W. Knocklein, and Dr. Mehdi Siami collected and analyzed limnological data.

Dr. Niles R. Kevern provided equipment, laboratory and office space. This work was supported by the U.S. Fish and Wildlife Service and the U.S. Army Corps of Engineers through grants to Drs. Charles R. Liston and Clarence D. McNabb and by the U.S. Geological Survey through a grant to Dr. William Taylor. Partial support was provided by the Agricultural Experiment Station, Michigan State University.

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CHAPTER ONE

Demographics and Life History of the Damselfly *Lestes disjunctus disjunctus* in the St. Marys River, Michigan.

INTRODUCTION

Odonata inhabiting fresh-water littoral environments are often numerically abundant and represent a relatively large proportion of the invertebrate biomass (Benke 1976; Crowder and Cooper 1982). This abundance, along with the predaceous habits of, nymphs has stimulated interest in qualitative life history and behavioral studies, as well as analyses of diets (Corbet 1962, 1980). More recent work has focused on either the potential functional role of Odonata in littoral systems or inter-odonate or odonate-fish interactions as possible factors regulating populations (Benke 1978; Johnson and Crowley 1980; Johnson et al. 1985). However, few studies have attempted to quantitatively examine population dynamics of Odonata (Lawton 1970; Benke and Benke 1975). Demographic analysis of aquatic insect populations are rare. The only study of Odonata to quantify survival in all life stages is Ubukata (1981).

During the past few decades, ecological research has been increasingly directed toward quantitative approaches. However, basic life history information is often lacking for these studies (Rosenberg 1975). Corbet (1954) recognized two basic types of life histories for Odonata: "spring species" that spend the winter in final instar diapause, then emerge synchronously in spring or "summer species" that spend the winter in early instars and emerge asynchronously throughout the summer. It is now recognized that a wide range of life history types exist between these two extremes (Paulson and Jenner 1971). Previous studies of *Lestes disjunctus disjunctus* Selys indicate it spends the winter in the egg stage in diapause, hatches in early spring, and emerges relatively synchronously in mid-summer (Sawchyn and Gillott 1974a). The developmental pattern of discrete life stages present during separate seasons and relatively synchronous and rapid development makes *L. d. disjunctus* an attractive species for the study of odonate demographics.

This chapter presents results of a demographic analysis of a natural population of *L. d. disjunctus* using life table techniques. Ancillary data, both quantitative and observational, which relate to interpretation of population or life history phenomena have been included. Related studies, presented in chapter two, examine the influence on nymphs of water temperature, prey density, and interactions with other predators as well as the influence of fish on habitat selection as possible mechanisms regulating population size of *L. d. disjunctus*.

AREA OF STUDY

The St. Marys River originates at Whitefish Bay, Lake Superior and flows southeast 113 km to Lake Huron (Figure 1). The drainage basin, which encompasses an area of 2,367 km^2, is comprised of till and lacustrine sediments overlying bedrock of Precambrian origin in the east grading to Ordovician age shale and Silurian age Niagaran Dolomite in the west (Dorr and Eschman 1970). The basin is largely undeveloped in the south and moderately developed in the north. The twin cities of Sault Ste. Marie, Ontario and Michigan with a combined population of approximately 100,000 constitute the single population center within the basin.

Between the twin cities of Sault Ste. Marie, a portion of the river is diverted through a system of navigation locks and power canals with the remainder flowing over an extensive rapids. Below the St. Marys Rapids the river is divided into several channels and broad expanses by a series of islands. Average gradient throughout the river system is 6.0 $cm \cdot km^{-1}$, however, most of this drop in elevation (6.0 m) occurs at the rapids and navigation lock complex. River discharge is controlled at the rapids and navigation lock complex by compensating structures. Annual discharge during the period 1960 through 1980 averaged 2,202 $m^3 \cdot s^{-1}$ (Quinn and Kelly 1983). Average monthly discharge during the period of study ranged from 1,229 to 2,979 $m^3 \cdot s^{-1}$ (Table 1).

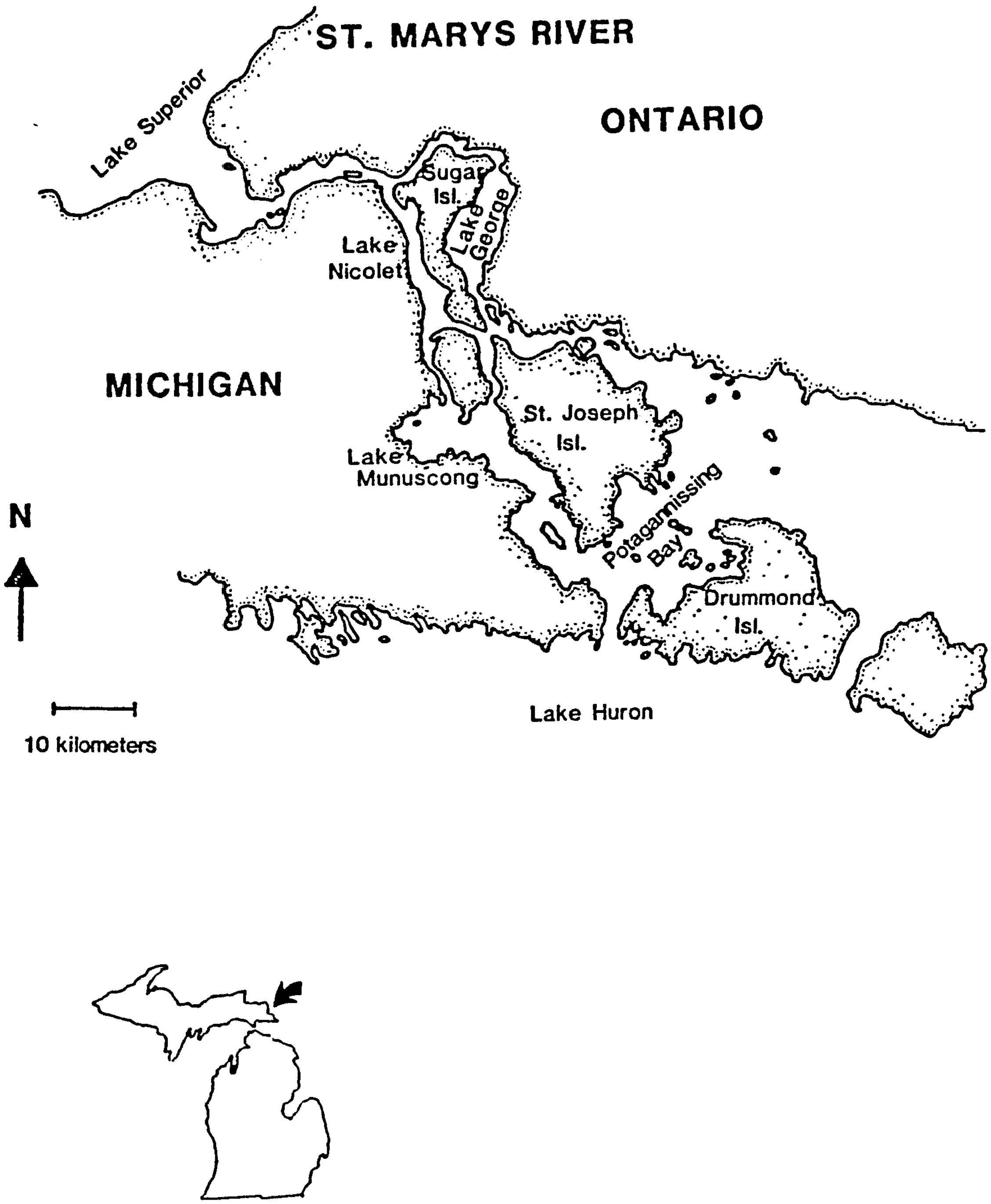

Figure 1. Map of the St. Marys River, Michigan and Ontario

Table 1. Average monthly discharge rates ($m^3 \cdot s^{-1}$) for the St.Marys River, Michigan during January, 1982 through September, 1983 (NOAA, GLRL unpub.).

month	1982	1983
January	1,229	2,291
February	1,286	2,314
March	1,286	2,452
April	1,305	2,424
May	1,730	2,922
June	2,101	2,951
July	2,078	2,911
August	2,387	2,979
September	2,398	2,398
October	2,534	
November	2,837	
December	1,382	

Lake Nicolet receives approximately 65% of this discharge, with the remainder flowing around Sugar Island into Lake George (McNabb et al. 1983). Lake Nicolet has a surface area of 3,958 ha, water depth averages approximately 3 m except in the navigation channel, which is maintained at a minimum 8.6 m depth by dredging. Water retention time within the Lake Nicolet basin was determined to be only 21.6 hours by McNabb and colleagues (1983). Where the shoreline is protected from wind and water currents, extensive emergent wetlands (Cowardin et al. 1979) have developed.

A site within the emergent wetlands on the west side of Lake Nicolet in the St. Marys River, approximately 18.5 km south of Sault Ste. Marie, Michigan, was selected as the area of study. Map coordinates were 49° 20' 19" N and 84° 13' 30" W. The study site encompassed an area of 4.03 ha extending from the shore to a depth of approximately 1.0 m. However, water depth varied during both years, as river discharge and meteorologic conditions varied (Figure 2).

The predominant aquatic macrophyte within the study area was bur reed, Sparganium eurycarpum (Table 2, Figure 3). Both bur reed and hardstem bulrush, Scirpus acutus, form extensive beds along the west shore of Lake Nicolet. Type and location of emergent macrophytes present in the area are shown in Figure 3, with estimates of the area occupied presented in Table 3. Submersed macrophytes in the area consisted mostly of Potomogeton gramineus, and Ranunculus spp.

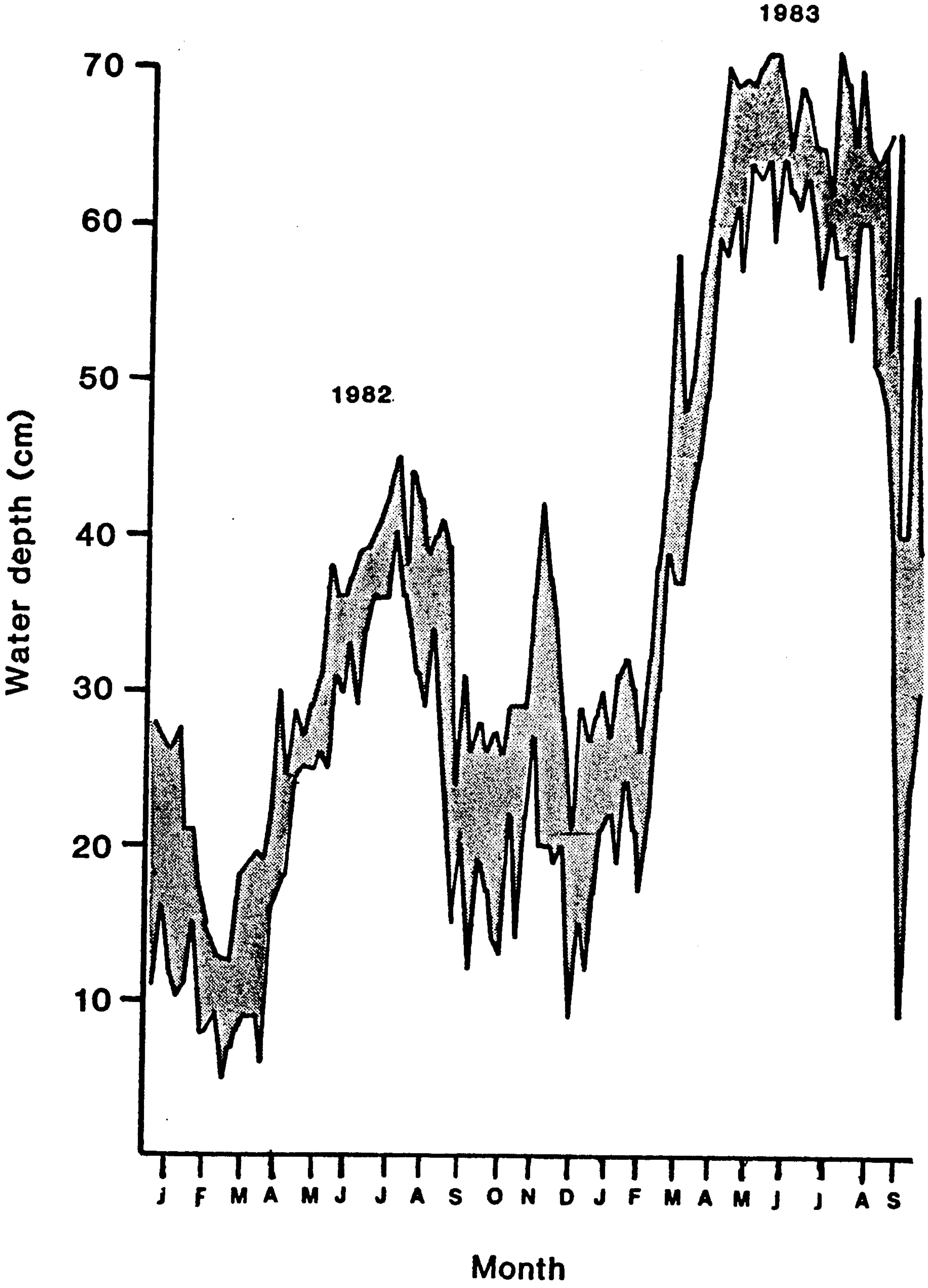

Figure 2. Weekly range in water level at the center of the study area in 1982 and 1983.

Table 2. Key to species of mixed stands of emergent vegetation in the west littoral zone of lower Lake Nicolet, St. Marys River shown in Figure 3. (Adapted from McNabb et al. unpub.).

Map Designation	Species Combinations
A	*Scirpus acutus* *Eleocharis smallii*
B	*Scirpus acutus* *Sparganium eurycarpum*
C	*Sparganium eurycarpum* *Typha latifolia*
D	*Sparganium eurycarpum* *Phragmites australis*
E	*Sparganium eurycarpum* *Scirpus acutus* and/or *Eleocharis smallii*
G	*Sparganium eurycarpum* Graminaceae
H	*Scirpus americanus* *Scirpus acutus* and/or *Eleocharis smallii*
I	*Sparganium chlorocarpum*
J	Other(s)

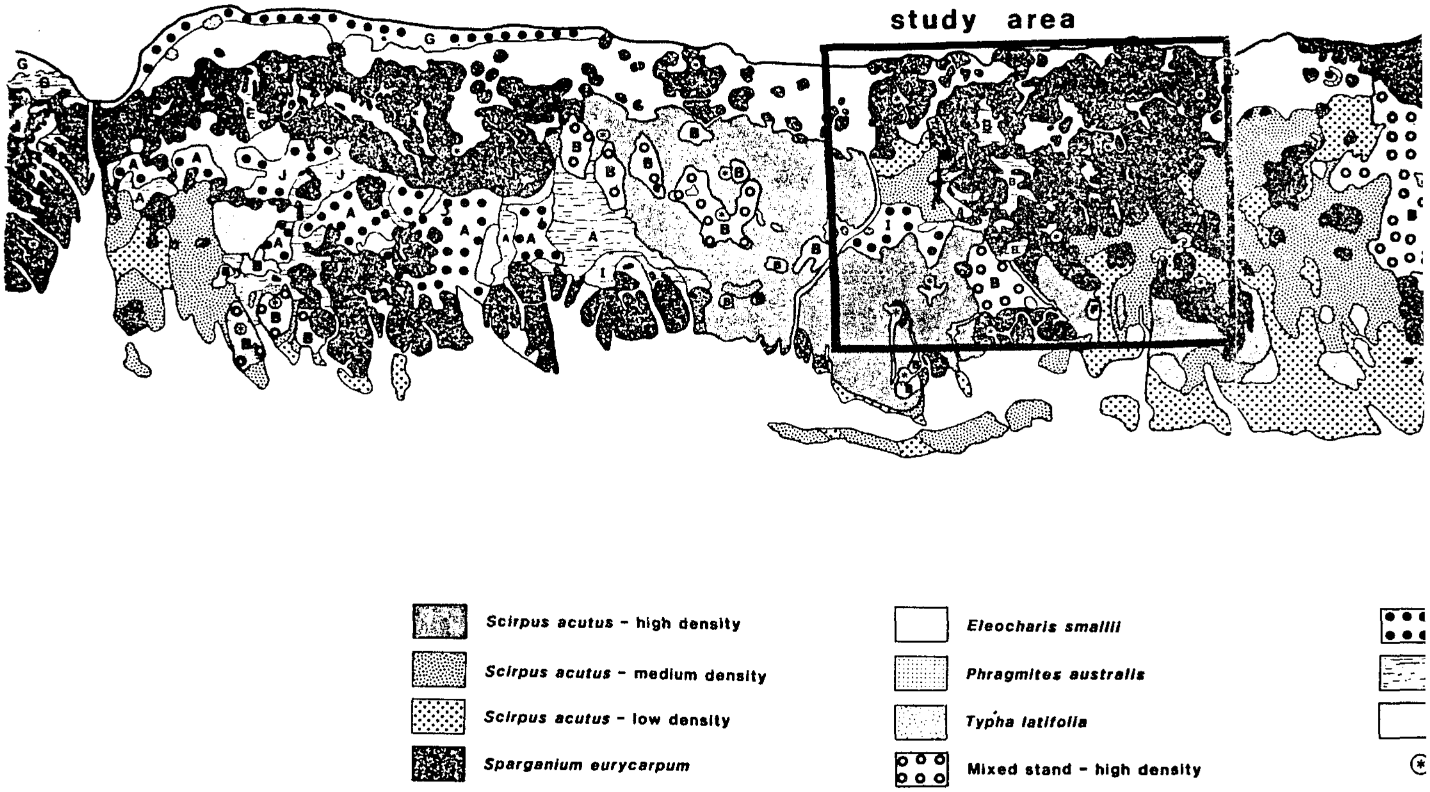

Figure 3. Distribution of aquatic macrophytes in the west littoral zone of lower Lake Nicolet, St. Marys River, including the study area. (McNabb et al. unpub.).

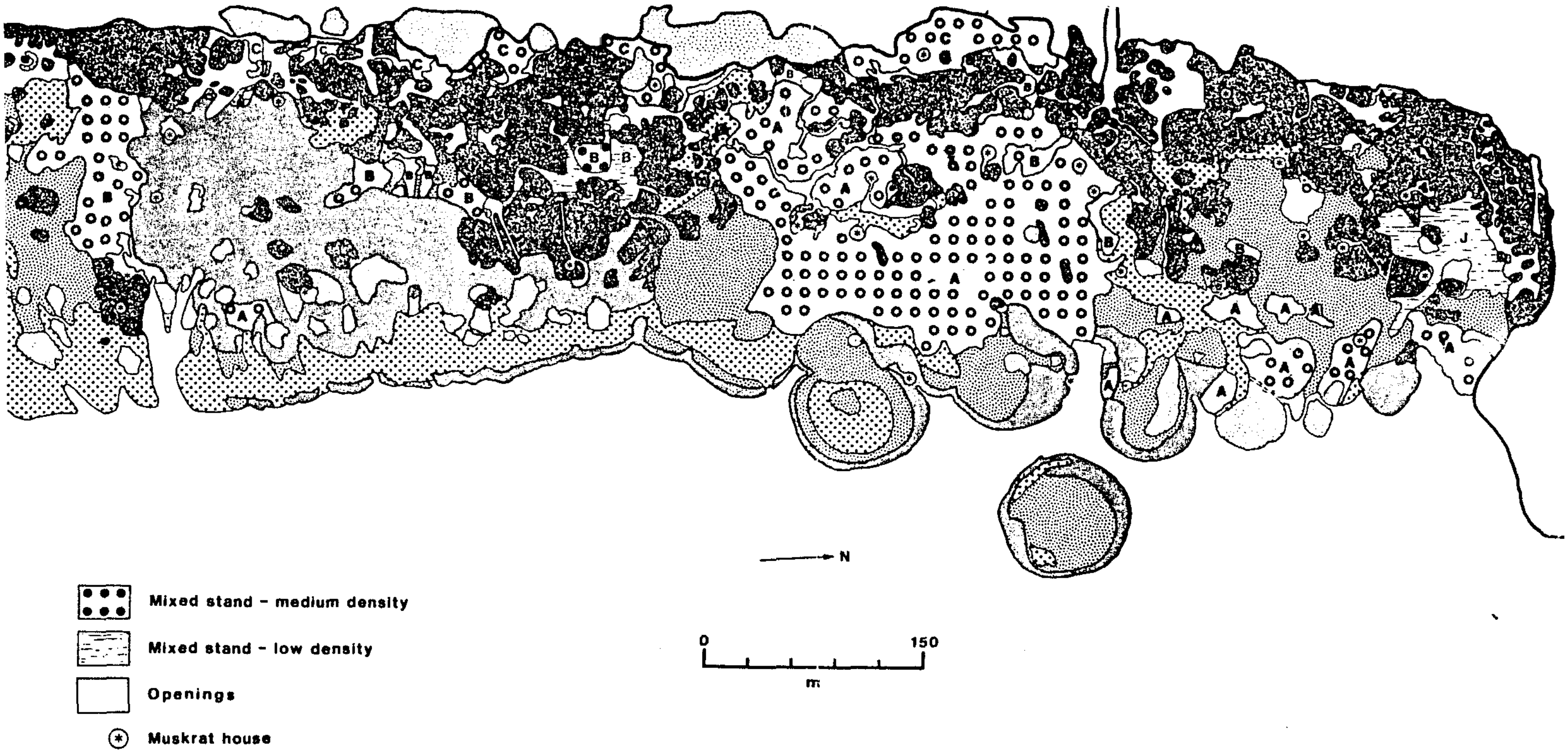
A
B
C
J
N
0
150
m
Mixed stand - medium density
Mixed stand - low density
Openings
Muskrat house

Table 3. Area of emergent vegetation and open water occupying the west littoral zone of lower Lake Nicolet, St. Marys River. (McNabb et al. unpub.).

Vegetation Type	Density	Area (hectares)	Percent Total
Scirpus acutus	High	6.67	15
	Medium	5.31	11
	Low	3.97	9
Sparganium eurycarpum	-	12.59	28
Eleocharis smallii	-	1.37	3
Typha latifolia	-	0.85	2
Mixed stand (A)	High	3.66	8
	Medium	0.76	2
	Low	0.57	1
Mixed stand (B)	High	1.77	4
	Medium	0.39	< 1
Other mixed stands (C-J)	High	0.74	2
	Medium	0.75	2
	Low	0.75	2
Open water	-	5.16	11

MATERIALS AND METHODS

Physical-Chemical Measurements

Water quality parameters were measured monthly within stands of bur reed at the north edge of the study area. Dissolved oxygen was measured using the azide modification of the Winkler titration, alkalinity using methyl orange titration, turbidity using a Hach model 2100 turbidimeter, pH using a combination electrode, phosphorus colorimetry after by acid digestion, and nitrogen by the Kjeldahl method. Methods used are described fully in Standard Methods for the Examination of Water and Wastewater (APHA 1980).

Water temperature was monitored during 1982 and 1983 using a Ryan model 600 recording thermometer, located at the center of the study area. Thermograph tapes were changed weekly and average daily water temperature calculated from temperatures recorded at 0400, 0800, 1200, 1600, 2000, and 2400 hours. From January through February, ice extended through the water column and 10 to 20 cm into the sediment. An effort to record ice temperature during this period was made, but periodic thawing and refreezing made retrieval of the recording thermometer without damage difficult.

Area of Cover

Sampling during 1982 suggested that nymphs of Lestes disjunctus disjunctus inhabited two types of cover within the study area. These included beds of bur reed and mats of dead emergent macrophytes from the previous years growth which floated on the surface. To quantify population size of nymphs in the study area, the aerial extent of each habitat was determined.

Area (m^2) of dead matted vegetation was determined by measuring the width of the mat at 10 m intervals along shore. For mats not associated with the shoreline both length and width was measured at intervals short enough to define mat shape, usually 5 to 10 m.

Dead matted vegetation unexpectedly proved to be a dynamic habitat. Initially mats of vegetation were scattered throughout the littoral zone. However, rising water levels and spring storms floated some mats offshore, while concentrating the remainder toward shore where wave action served to intertwine stems forming a single thick mat bordering the shoreline. During the course of the summer this mat began to decay and sink to the bottom. Decay of this vegetation became quite rapid in June and little floating dead vegetation remainded by July. It was therefore necessary to take measurements of the dead vegetation mat cover each time population samples were collected.

The area (m^2) of bur reed beds within the study area was determined using polar planimetry of habitat maps drawn from low altitude photographs taken in 1982. Ground truthing during 1983 suggested neither the extent nor the configuration of bur reed beds had changed appreciably since 1982.

Population Sampling

Egg Stage

Population size of the egg stage was estimated using two separate techniques. The first method involved determining fecundity of adult females, then combining these data with adult population estimates to obtain an estimate of the total number of eggs oviposited in the study area. The second technique for estimating egg population size also provided information on egg mortality.

Method 1: Adult females to be used for ovarian analysis were collected weekly using an aerial net, sacrificed in a collecting jar containing chloroform, and returned to the laboratory. Total length and color of each female was recorded on a numbered envelope, the individual placed in the envelope, and frozen until ovaries could be examined. When examining ovaries, a female was placed in a petri dish containing water, the abdomen severed from the thorax, and the sternum removed. Abdominal contents were then removed, ovaries separated from other tissue, and teased apart. All eggs which could be discerned under a stereozoom binocular microscope were counted.

Odonata have a panoistic type ovary in which successive batches of eggs may mature following an oviposition episode. However, it is unlikely that a female will live long enough to oviposit her full compliment of eggs (Corbet 1962). Therefore, total egg counts provide an estimate of potential fecundity rather than an estimate of realized fecundity. To derive estimates of fecundity or the number of eggs oviposited, a method suggested by Corbet (1962, p. 27) was employed. In this method, the number of eggs at successive ages are subtracted from the number of eggs found in pre-reproductive individuals. The difference is then used as an estimate of total eggs oviposited. Three age classes of adults were recognized: pre-reproductive, reproductive, and post-reproductive. Age was determined using color changes associated with aging (Corbet 1962).

Method 2: This method involved collecting and hatching eggs following oviposition. Lestes disjunctus disjunctus oviposits endophytically in emergent macrophyte tissue 10 to 20 cm above the water surface. In September 1982, following the completion of oviposition, 0.25 m^2 plots of bur reed were collected from the study area. The upper portion of the plant, extending to 20 cm below the water surface was taken to insure collection of all eggs. Five samples were collected from each of 4 strata including; the shoreline and 25, 50, and 75 m offshore.

Plant stems collected were returned to the laboratory and refrigerated at 1°C for 100 days to insure completion of egg diapause. When removed from the refrigerator, stems were placed in aquaria containing tepid tap water. Temperature was controlled at 20°C, aquaria water filtered daily through a 150 μ sieve, and newly hatched nymphs recorded. Nymphs capable of orienting their body so as to stand and capable of movement were classified as alive. The weighted mean number of nymphs hatching per unit area was then multiplied by the area (m^2) of bur reed within the study area to estimate viable egg population size in September (see nymph stage methods for discussion of weighted mean).

In April 1983, ten 0.25 m^2 samples of dead matted vegetation from the previous years growth were collected from the study area. At this time, stems of live macrophytes had not emerged from the sediment. Stems of dead vegetation were not refrigerated, but placed in aquaria containing tepid tap water and incubated at 20°C. Methods to determine the number and condition of nymphs hatching were identical to September collections. The mean number of nymphs hatching from April samples was multiplied by the area of matted vegetation (m^2) to estimate egg population size at that time. The difference in egg population size between September and April was assumed to be overwintering mortality in the egg stage.

Percent of nymphs hatching per day was calculated from stems collected in April and incubated at 16 and 20°C. These data in combination with data published for hatching rates of L. d. disjunctus incubated at 12 and 15°C (Sawchyn and Church 1973) were used to develop a regression equation which would predict hatching rate as a function of temperature. The intercept of the regression line was interpreted as the threshold temperature for L. d. disjunctus.

Nymph Stage

Sampling for nymphs was initiated when cumulative degree days recorded in the field neared egg development times determined in the laboratory. Beginning on May 1, samples were collected from the dead vegetation mats every 2 days until nymphs were found. Following the appearence of nymphs, a more rigorous sampling scheme was initiated.

The dynamic nature of each strata, combined with the behavior of nymphs, prevented the allocation of sampling effort in proportion to the area of each strata. Early instar nymphs occur exclusively in the dead matted vegetation from which they hatch and remain in this strata for several weeks. As aquatic macrophytes begin to develop, nymphs disperse, with many moving to the dense bur reed beds. Because of this, initial sampling effort was limited to the dead vegetation strata and later expanded to include the bur reed strata.

Sampling in both strata was conducted at 3 to 4 day intervals, with several exceptions, until nymphs reached instars IX and X. Sampling was then conducted weekly. On each date, a minimum of 12 samples was collected from each strata sampled. Sample locations were selected randomly from a map of the study area gridded into 1 m^2 units. In the field, a series of poles with surveyors flags was placed along a grid of 50 m intervals to aid in locating sample sites.

Sampling within the bur reed strata was accomplished using a modified Gerking sampler (Mittelbach 1980). This sampler consisted of a plexiglass box with sliding doors attached to the bottom and a 150 µ plankton net attached to the top (Figure 4). The inner edges of the sliding doors were sharpened to pinch off plant stems when closed. However, thick fibrous stems of bur reed could not be severed easily and a knife was used for this purpose.

In collecting a sample the operator walked slowly toward the sample location holding the sampler above the emergent vegetation with the doors in the open position. Upon arriving at the desired location, the samper was lowered over the emergent stems and pushed gently through the water column to the sediment surface. The doors were then closed as forcefully as possible, the sampler rotated toward the collector, and a knife used to sever plant stems. The sampler was then lifted from the water with the doors facing upward. Macrophytes were removed from the sampler and placed in an 18 L pail and the remaining contents of the sampler rinsed into the plankton net collecting jar.

The Gerking sampler proved ineffective in sampling the dead floating vegetation because leaves and stems of bur reed and bulrush had become intertwined so as to form a matrix. Pushing the Gerking sampler through these mats was not possible. Consequently this strata was sampled using a 0.3 m

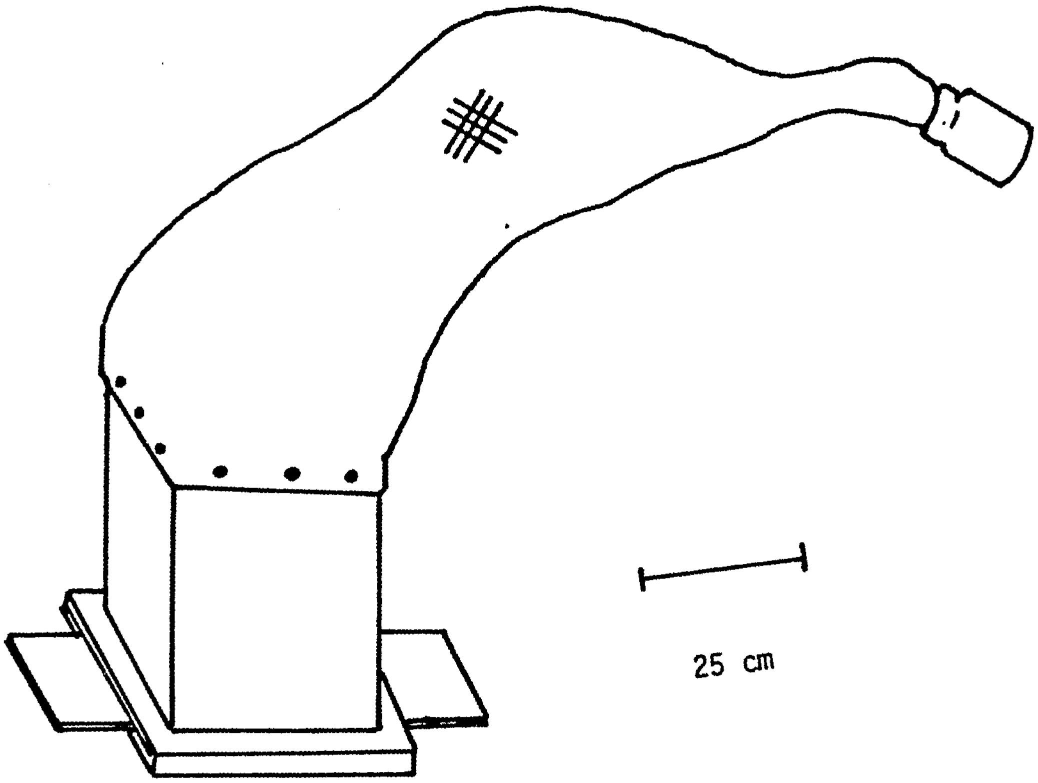

Figure 4. Modified Gerking sampler.

diameter plankton net of 70 µ mesh attached to a circular net frame on a wooden handle.

In collecting a sample, the cod end of the plankton net and the handle were held in one hand so as to close the net mouth. The net was lowered to the bottom, pushed forward about 1 m, and lifted quickly from the bottom through the mat. Excess stems hanging beyond the net diameter were trimmed using scissors. Treatment of samples following collection was identical to the treatment of Gerking type samples.

Following collection, samples were returned to the laboratory and nymphs sorted while still alive. Sorting was usually completed within 24 hours of collection. In sorting nymphs, a small amount of sample water was placed in a pyrex baking dish and examined over a light table. The volume examined at any one time was adjusted so that the bottom of the dish remained visible. Plant stems were cut into short sections of 20 to 25 cm, floated in tap water in the dish, and examined for nymphs. Number of nymphs collected was converted to number$\cdot$m^{-2}.

When sampling two strata, a weighted average and its associated variance was calculated (Sokal and Rohlf 1969):

$$\bar{N} = N_1w_1 + N_2w_2/w_1 + w_2$$

$$s^2 = x^2{}_1 + x^2{}_2/(n_1-1)(n_2-1)$$

where $\bar{N}$ = weighted average, $N_{1 \cdot \cdot 2}$ = number in strata 1 or 2, $w_{1 \cdot \cdot 2}$ = weighting factor (proportion of the total sampling area) for strata 1 or 2, and s^2 = variance of $\bar{N}$.

Nymphs sorted from samples were identified to species using a stereozoom binocular microscope, (10 - 70X). Taxonomy followed Walker (1953). Total length, excluding caudel lamella, and head width were recorded for 20 or more nymphs for each sampling date.

Exuvia

Number of nymphs molting to adults were estimated by counting exuvia in the study area. Exuvia were counted in two sub-strata within bur reed strata; 1) the outer edges of plant beds consisting of medium cover and 2) the center of plant beds which consisted of heavy cover. Ten plots (1.0 m^2) were established in each strata and exuvia collected from plant stems weekly or more frequently, if rain was anticipated. A weighted average number of nymphs molting$\cdot m^{-2}$ was calculated from these data and multiplied by the area of bur reed to estimate nymphs molting in the study area.

Adult Stage

Population estimates for adults were made using mark and recapture techniques. Following emergence, tenneral adult _L. d._ _disjunctus_ flew to the treeline, 70 to 100 m from the waters edge and remained there for several days before returning to the water. Marking was not initiated until individuals had returned to the study area. This insured that individuals had hardened and minimized mortality due to handling.

Marking was accomplished using a red colored "Sharpie" felt tip marker. Marks consisted of a series of dots and dashes applied to one or both wings. This code was changed daily and allowed the collector in the field to distinguish the date an individual had been marked. Both marking and recapturing were conducted daily between 0800 and 0930 hours by walking a prescribed area within the study area. On each date the number of each sex marked was recorded, as well as those recaptured and the date of release of recaptures.

Adult population estimates were calculated from mark and recapture data using a modification of the Peterson population estimate (Begon 1979):

$$\hat{N}_i = [M_i(n_i + 1)/(m_i + 1)]$$

where $\hat{N}_i$ = the estimated population size on day i; $n_i + 1$ = the number of individuals caught on day i + 1; $m_i + 1$ = the number of marked individuals caught on day i + 1; and M_i = the number of marks at risk on day i consisting of individuals marked from day i-6 to day i-1 (the total number of marked individuals considered for population estimates). M_i was used in place of r_i (number marked on day i) of the normal Peterson estimate.

A standard error of the population estimate was calculated from:

$$\hat{SE}_N = \sqrt{M^2{}_i(n+1)(n-m)/(M+1)^2(m+2)}$$

To test the influence of handling and marking on survival, 40 individuals were collected, a wing mark placed on 20, and 20 individuals neither marked nor handled except for netting. Both marked and unmarked individuals were then released within a screen tent and survival monitored. Prey provided daily were predominantly mosquitoes.

Data Analyses

Age Specific Life Table

Construction of an age specific life table requires information on the total number of individuals that pass through a particular stage or instar. Field sampling provides information on the number of individuals observed on each sampling occasion only, which is a function of the total number entering a stage and the probability of surviving to be sampled. Because of this the total number of individuals entering a stage must be estimated using statistical techniques. A method developed by Richards and Waloff (1954) was used to estimate stage recruitment. This method assumes a single pulse of recruitment and consists of plotting the regression of decreasing numbers with time after peak abundance. This regression line is then extended back to the time when the stage was first found (t_1) and the population corresponding to time t_0 is the number of individuals alive just before the stage is seen for the first time (Southwood 1978).

Stage recruitment data were then used to construct a life table to further describe the data. For ease of interpretation, stage recruitment data were initially set at 1,000 individuals. The life table then contained the following columns (Deevey 1947):

x	The pivotal age (egg, instar, or adult)
l_x	The number surviving at the beginning of a stage
d_x	The number dying during the age interval x, ($l_x - l_{x+1}$)
q_x	The proportion dying during the interval x to x+1
T_x	The total number of age units beyond the age x or the life remaining to those at age x which is given by: $T_x = L_{x1} + L_{x2} + \cdots L_{xw}$ where L_x = number alive between age x and x + 1 and w = the last stage
e_x	The expectation of life at age x which is given by: $e_x = T_x / l_x$

m_x The average number of eggs oviposited per female.

Population Rate of Increase

The net reproductive rate (R_0) was calculated from survival (l_x) and age specific fertility (m_x) data where:

$$R_0 = \Sigma l_x m_x$$

Additionally, data from adult and egg population estimates during 1982 and 1983 enabled the calculation of the population rate of increase (λ) for the population under natural conditions. With non-overlapping generations, λ can be shown to be comparable to the intrinsic rate of increase (r) for populations with overlapping generations (Southwood 1978):

$$N_t = N_0 e^{rt} = \lambda^t N_0$$

$$e^{rt} = \lambda^t$$

$$e^r = \lambda$$

$$r = \ln \lambda$$

With non-overlapping generations $\lambda^t = R_0$.

RESULTS

Physical-Chemical Measurements

River water at this location was soft and low in both total phosphorus and total nitrogen. Dissolved oxygen levels decline to around 8 $mg \cdot L^{-1}$ by mid-summer, but remained above 90% saturation during all seasons. Turbidity and pH fluctuated only moderately during the open water period (Table 4).

Water temperature began to rise in April with the period of initial warming to 10°C being rapid (8 to 9 days) during both years. Following this initial warming period water temperatures fluctuated, but rose steadily through mid-July (Figure 5). Water temperature began to decline by August in both years. Maximum average daily water temperatures recorded in 1982 and 1983 were 22.3 and 26.9°C, respectively.

Area of Cover

Floating mats of dead vegetation provided the only cover in the study area until aquatic macrophytes began to develop in early June, 1983 (Table 5). The area of dead vegetation mats was 7,769 m^2 at ice out. This was reduced to 6,008 m^2 (-22.7%) in late April when rising water levels caused mats to float above the substrate and stems to which they had been anchored, allowing some to drift offshore. This cover

Table 4. Summary of physical and chemical parameters measured monthly in the west littoral zone of lower Lake Nicolet, St. Marys River during 1982 and 1983.

	D.O. (mg/L)	pH (s.u.)	Alk. (mg/L)	Turb. (NTU)	Total P (mg/L)	Total N (mg/L)
			1982			
May	11.8	8.20	n.d.	5.37	n.d.	n.d.
June	9.9	7.24	n.d.	1.85	.008	.066
July	9.4	7.86	n.d.	2.49	.009	.332
August	8.0	7.57	n.d.	2.70	.017	.228
September	9.2	7.42	n.d.	3.18	.082	.681
October	9.1	7.63	37.5	2.83	.114	.710
November	11.1	7.50	40.0	3.52	n.d.	n.d.
			1983			
April	10.9	7.89	41.0	n.d.	n.d.	n.d.
May	10.5	8.06	39.4	3.45	n.d	n.d.
June	8.3	8.14	38.2	2.68	n.d.	n.d.
July	7.8	7.53	39.1	2.30	n.d.	n.d.
August	7.7	7.48	39.2	2.37	n.d.	n.d.
September	7.9	7.59	39.2	2.69	n.d.	n.d.
October	9.2	7.86	39.0	3.10	n.d.	n.d.
November	10.2	n.d.	n.d.	3.50	n.d.	n.d.

n.d. = no data

remained somewhat stable until mid June, when the dead stems began to decay. Stem decay was rapid from 13 June through the end of sampling, resulting in near total loss of dead vegetation cover by 13 July 1983.

Both bur reed and hardstem bulrush leaves reached the water surface the first week of June. The most abundant emergent aquatic macrophyte within the study area was bur reed (Table 5). Distribution of bur reed was nearly continuous at the north edge of the study area and fragmented by pockets of open water elsewhere (Figure 3).

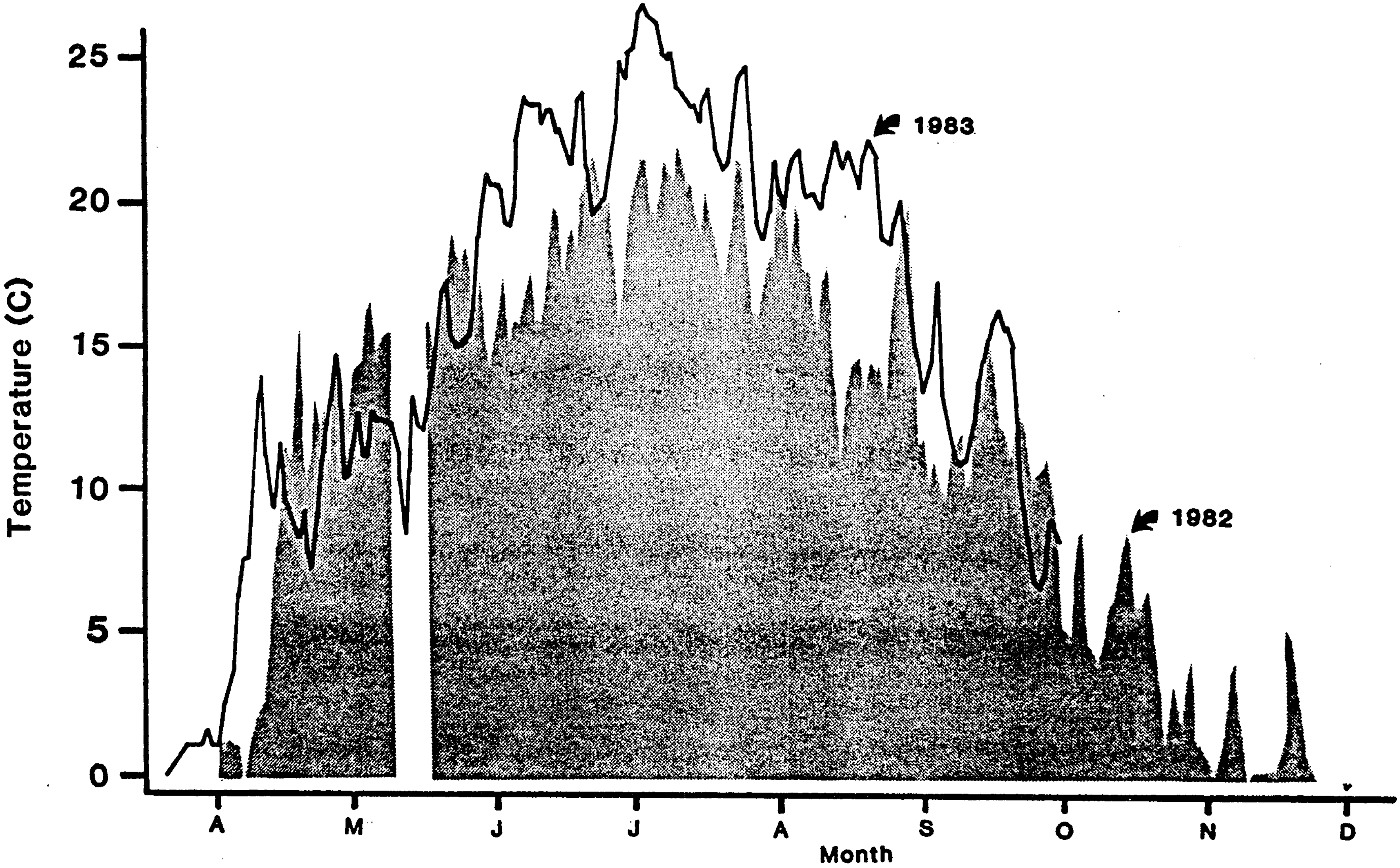

Figure 5. Average daily water temperature in the study area during 1982 and 1983.

Table 5. Area (m^2) of emergent macrophytes and other predominant cover types in the study area during May, June, and July 1983.

Date	*Sparganium eurycarpum*	*Scirpus acutus*	Mixed vegetation	Dead Veg. Mats	Open Water
May 14				6,008	37,192
17				6,008	37,192
20				6,008	37,192
24				6,008	37,192
27				6,008	37,192
June 2				6,008	37,192
9	15,192	5,787	4,403	6,008	5,802
13	15,192	5,787	4,403	6,008	5,802
17	21,200	5,787	4,403	3,140	5,802
22	21,200	5,787	4,403	1,380	7,562
26	21,200	5,787	4,430	740	8,202
29	21,200	5,787	4,403	580	8,362
July 6	21,200	5,787	4,403	360	8,582
13	21,200	5,787	4,403	176	8,766

Demographics

Egg Stage

Ovaries collected from 47 adult females in 1982 and 65 collected in 1983 were examined to determine potential fecundity. Differences in the number of eggs per age group among years were non-significant in all comparisons (Mann-Whitney U-test $P > 0.05$, Table 6). While pre-reproductive adults in 1982 averaged 25.7% more eggs per female than those collected in 1983, differences were largely the result of one single individual bearing 219 eggs. Standard errors associated with means were relatively low, excepting

Table 6. Descriptive statistics for eggs carried by female <u>Lestes disjunctus disjunctus</u> collected in the study area during 1982 and 1983.

	1982			1983		
age	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.
Immature	21			15		
Pre-reproductive	9	105.5	23.8	20	83.9	5.2
Reproductive	10	47.0	6.5	20	47.0	3.5
Post-reproductive	7	32.0	6.5	10	38.7	4.3
Δ (Pre - Post)		73.5			45.2	

pre-reproductive adults in 1982, suggesting little variation in eggs per female by age class.

The weighted mean from areas 25, 50, and 75 m offshore in September 1982 and the mean number of eggs hatching from dead vegetation collected in April 1983 were determined (Table 7). No eggs hatched from bur reed stems collected in the shoreline sub-strata during September, 1982. Later observations confirmed that females did not oviposit along shore and data from the shoreline samples were subsequently omitted in calculating weighted mean number of eggs hatching from bur reed. Data were variable during both years with ranges of 0 to 1,344 eggs$\cdot$m^{-2} in 1982 and 22 to 1,199 eggs$\cdot$m^{-2} in 1983. Differences in egg density were non-significant for both among-seasons and among strata comparisons (Mann-Whitney U-test $P > 0.05$).

Egg hatching rate, as percent of eggs hatching per day, was positively correlated with water temperature (Figure 6).

Table 7. Descriptive statistics for Lestes disjunctus disjunctus eggs hatched from Sparganium eurycarpum leaves collected in the study area in September, 1982 and dead vegetation collected in April, 1983.

	September, 1982	April, 1983
n	15	10
$\bar{x}$ Alive	183.5	343.2
S.E.	90.3	131.0
% Dead	6.0	3.4

A linear regression of hatching rate against incubation water temperature gives an equation of:

$$\% \text{ eggs hatching/day} = -1.63 + 0.38(T),\ r^2 = 0.95$$

The regression line intercepted the X-axis at 4.3°C which was interpreted as the threshold temperature.

Nymph Stage

Ten instars were determined using measurements of head widths from nymphs collected in the field and nymphs of known instar reared in the laboratory. Separation of instars 4 through 10 was possible utilizing a frequency distribution of head width measurements from the field data (Figure 7). However, slight differences in head widths of instars 1, 2, and 3 necessitated the measurement of laboratory-reared nymphs for separation (Table 8). Variation of head width

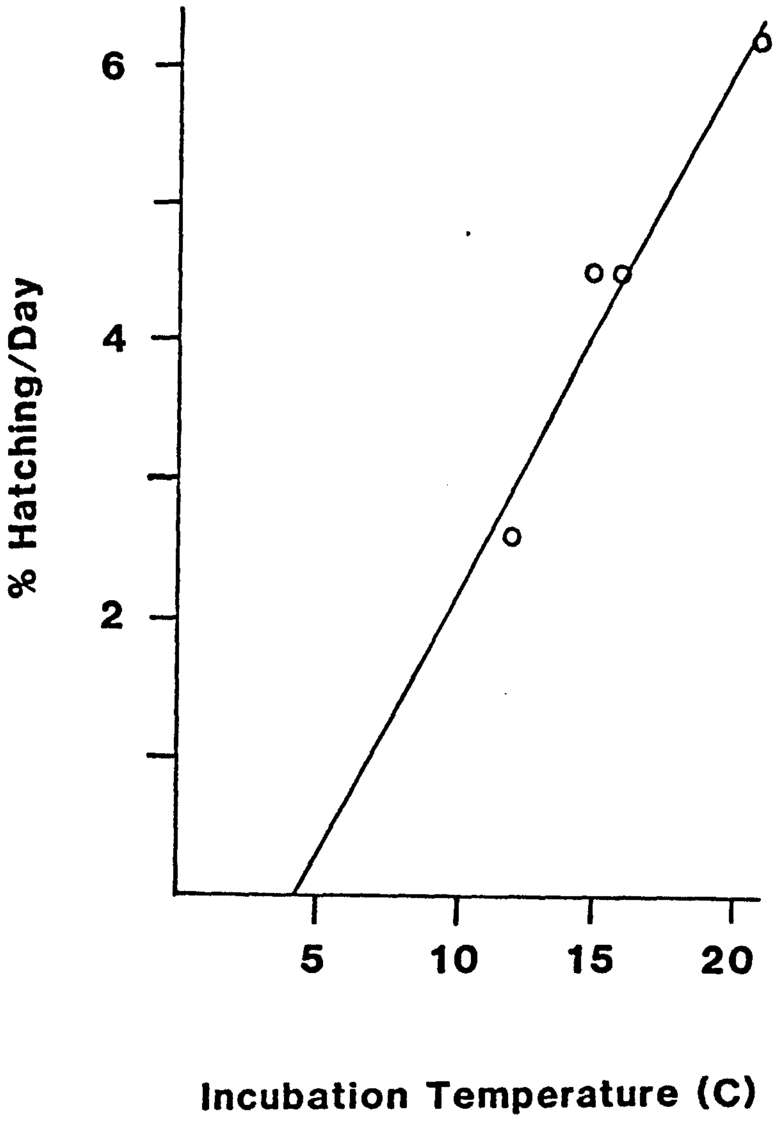

Figure 6. *Lestes disjunctus disjunctus* egg hatching rate as a function of water temperature.

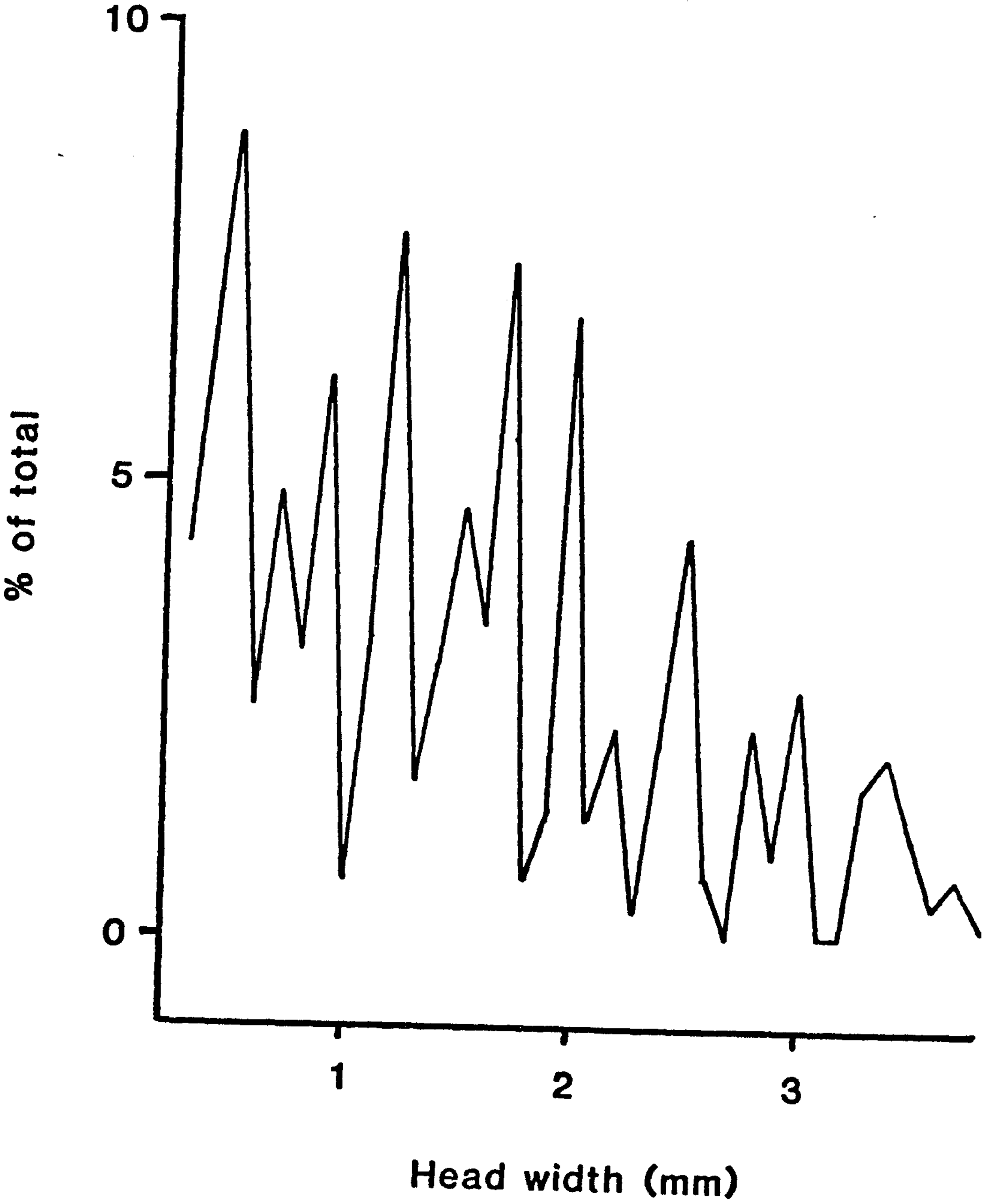

Figure 7. Frequency distribution of *Lestes disjunctus disjunctus* head width measurements.

Table 8. Head width measurements from *Lestes disjunctus disjunctus* nymphs from the study area and from nymphs reared in the laboratory.

	Field Data			Laboratory Data		
Instar	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n
I	0.37	0.01	28	0.34	0.00	5
II	0.51	0.01	25	0.43	0.00	5
III	0.61	0.01	38	0.64	0.02	7
IV	0.90	0.01	26	0.87	0.01	8
V	1.24	0.02	23	1.30	0.00	2
VI	1.54	0.02	22	1.55	0.05	4
VII	2.02	0.04	17	2.04	0.08	8
VIII	2.54	0.01	14	2.57	0.06	4
IX	3.07	0.01	21	2.94	0.03	6
X	3.60	0.02	26	n.d.		

measurements within instars increased with increasing instar, but was low for both field and laboratory data.

In 1982, preliminary sampling for nymph density estimates was conducted on 4 dates in 4 cover types, including; bur reed, hardstem bulrush, floating mats of dead vegetation, and mixed-species emergent macrophytes along shore. Cover present was similar to that present in 1983 except that vegetation mats were distributed throughout the area rather than located only along shore. Data were analyzed by collection date and cover type using a Mann-Whitney U-test (Table 9). Differences among bur reed and hardstem bulrush were significant on 11 and 18 June ($P < 0.05$). All other comparisons were non-significant ($P > 0.05$).

Table 9. Mean density (no$\cdot$m^{-2}) of Lestes disjunctus disjunctus nymphs collected from four cover types in 1982.

Plant Cover Type	Date 11 June n	x̄	18 June n	x̄	25 June n	x̄
S. eurycarpum	10	22.9	10	25.0	10	18.7
S. acutus	10	0.0	10	2.1	10	0.0
Veg. Mats	10	24.6	10	27.7	10	21.6
Mixed Vegetation	10	12.5	10	14.6	10	8.3

In 1983, nymphs were first on 14 May. They occurred exclusively within the dead vegetation strata through 13 June, before a portion emigrated to the bur reed. Density within the dead vegetation strata increased rapidly following initial hatching, with the seasonal maxima (105.8$\cdot$m^{-2}) occurring on 20 May (Table 10). Density within this strata declined slowly through 17 June, then declined more rapidly. Single sample density estimates ranged from 0 to 431$\cdot$m^{-2}.

Nymphs were first collected from the bur reed strata on 17 June. Dip netting, the week before this, produced low numbers of nymphs in bur reed stands 1 - 2 m from the dead vegetation mats. However, no nymphs could be located beyond this 1 - 2 m border and it was assumed that emigration from the dead vegetation mats had yet to begin. Density of nymphs within the bur reed strata was initially low (Table 10). Density in this strata increased slightly until emergence began, while continuing to decrease in the dead vegetation.

Table 10. Mean density ($no \cdot m^{-2}$) of _Lestes disjunctus disjunctus_ nymphs collected from two cover types in the study area during 1983.

Date		Dead Vegetation			_Sparganium eurycarpum_		
		n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.
May	14	6	12.8	6.2			
	17	12	87.4	21.3			
	20	12	105.8	24.1			
	24	12	105.4	21.3			
	27	12	95.1	23.8			
June	2	18	80.6	24.1			
	9	18	77.2	28.7	12	0.0	0.0
	13	18	72.0	21.0	12	0.0	0.0
	17	16	77.1	21.0	12	15.5	5.8
	22	16	37.4	9.9	12	20.7	7.1
	26	12	24.9	7.1	12	22.2	6.9
	29	12	12.0	6.0	12	22.3	6.0
July	6	12	5.2	2.7	12	8.7	3.9
	13	12	5.2	2.7	12	0.0	0.0

Differences in density of nymphs among strata were tested by date using a Mann-Whitney U-test. Significantly lower numbers of nymphs were found in the bur reed strata on 17 June ($P < 0.05$). Differences among strata on later dates were non-significant ($P > 0.05$).

Estimates of total population size by instar or stage frequency data were determined (Table 11). The population was composed entirely of first instars on 14 and 17 May. Instars II and III entered the population on 20 May followed by instar IV on 2 June. Development after 2 June was more rapid due to increasing water temperatures. Length of time specific instars were present in samples ranged from 15 days (instar VIII) to 20 days (instars IV and V), with the mean

Table 11. Estimated stage-frequency data for total *Lestes disjunctus disjunctus* nymphs within the 4.03 hectare study area in the St. Marys River during 14 May through 13 July, 1983.

Date	Day	I	II	III	IV	V	VI	VII	VIII	IX	X
May 14	1	116962									
17	4	219929									
20	7	579748	193250	193250							
24	11	289235	481296	192519							
27	14	173704	260558	434262							
June 2	19	39607	66249	323885	301801						
9	26		33843	167802	436425	66980					
13	30				197285	328809	131524				
17	34				110050	349918	168854	31631			
22	39				73656	97864	196241	122586	24723		
26	43					40438	112246	157244	134993	22745	22251
29	46					26516	17357	52552	105013	122941	69909
July 6	53							7076	7076	50090	121782
13	60									348	1043

being 18.5 days. Low numbers collected on the final sampling date are probably the result of emergence having begun between 6 and 13 July.

Exuvia

Exuvia were collected from high and medium density stands of emergent bur reed stems (Table 12). Ranges associated with means for heavy and medium bur reed were 0-5 and $0\text{-}3\cdot m^{-2}$ respectively. No exuvia were found in 2 of 10 quadrats from heavy cover and in 4 of 10 quadrats from medium cover. Although mean density of exuvia in heavy cover was roughly twice that of medium cover, differences in density among the strata were non-significant (Mann-Whitney U-test, $P > 0.05$).

Adult Stage

A total of 292 adults were marked during preliminary sampling in 1982. Because of relatively low numbers of males marked (100) and recaptured (5%) data were not adequate for population estimates of males. Recapture rate for 192 females marked in 1982 was 9.9%. Weighted mean population estimates for the periods 11 through 16 July and 17 through 23 July were 23,871 (SE = 7,826) and 19,694 (SE = 7,522), respectively.

In 1983 adult *L. d. disjunctus* were first observed in the study area on 11 July. However, emergence may have begun several days earlier. A total of 696 adults were marked in

Table 12. Number _Lestes_ _disjunctus_ _disjunctus_ exuvia$\cdot m^{-2}$ collected from stands of high and medium density _Sparganium_ _eurycarpum_ within the study area in 1983.

Plant cover	n	$\bar{x}$	S.E.
High Density	10	2.10	0.55
Medium Density	10	0.90	0.31

1983, 433 females and 263 males. Of 1,012 females captured 188 (18.6%) bore marks, while 64 of 570 males (11.2%) captured, were marked individuals. Average ages at recapture were 5.6 days for females (range 1 - 25) and 6.1 days (1 - 24) for males.

Estimates of female population size in 1983 ranged from 10,516 on 17 July to 732 on 4 August (Figure 8). Adult population size generally decreased with time as most emergence was completed in the first week. An increase in estimated population size during 26 to 28 July was most likely the result of windy conditions reducing recapture relative to the total number observed. This second peak was noted for both sexes. Estimates of male population size in 1983 ranged from 6,552 on 17 July to 1,053 on 1 August. Males were less abundant than females in the study area through 3 August, but slightly more common thereafter. Males also appeared to be more active, although movements were not quantified.

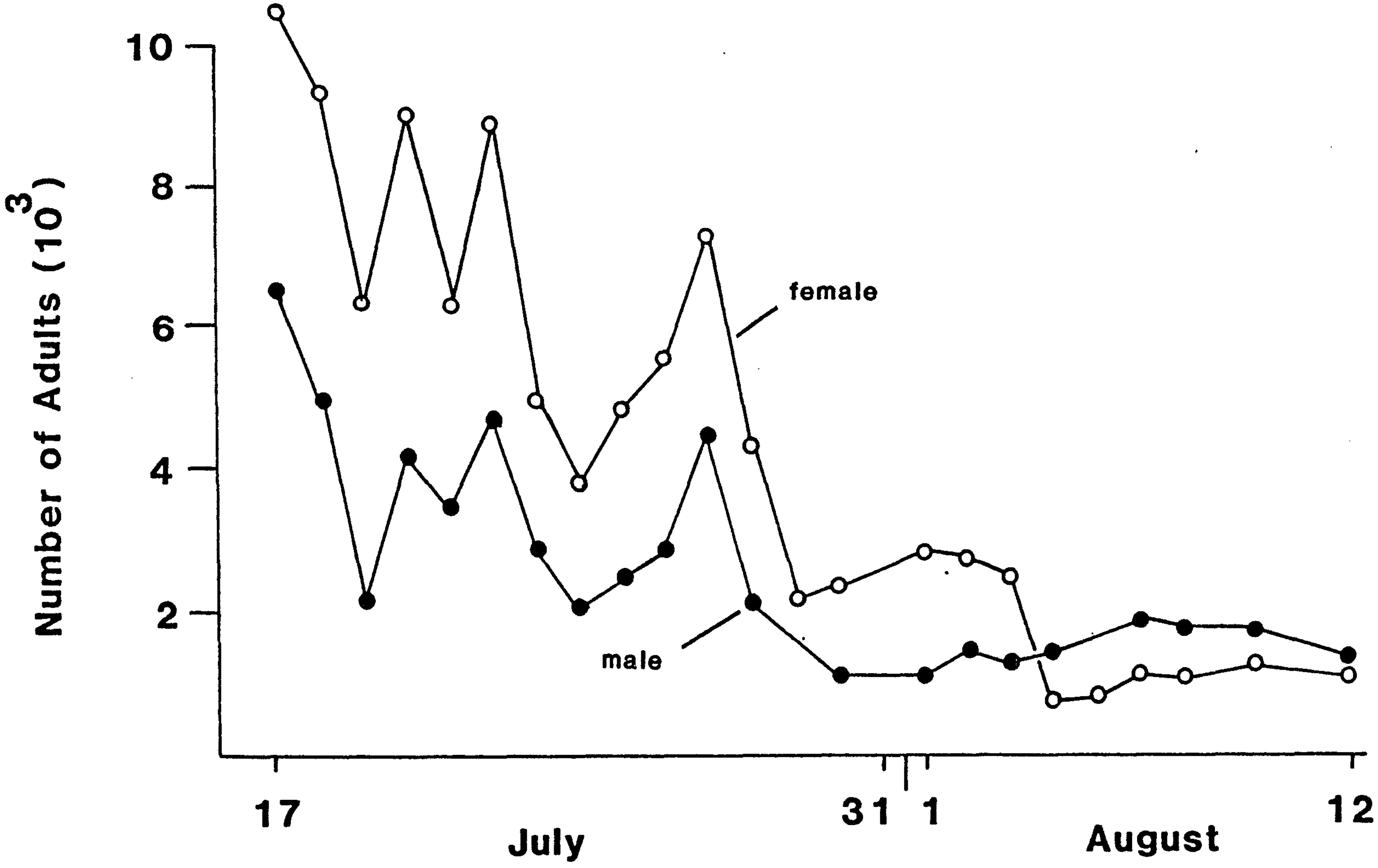

Figure 8. Estimated adult male and female *Lestes disjunctus disjunctus* population in the study area during 1983.

Emigration from the study area was measured in a 625 m^2 area adjoining the study area on 19 and 30 July 1983. On 19 July, 2 marked males along with 34 unmarked males and 43 unmarked females were captured. On 30 July, 3 of 31 males and 3 of 34 females were marked individuals (9.6 and 8.8% respectively).

Average age at death for adults held in a screened tent was 7.3 days (range 2 - 20), while marked adults averaged 5.6 days at death (range 1 - 18). Differences in mortality among marked and unmarked adults were non-significant (Kolmogorov - Smirnov test, $P > 0.10$). However, the observed D value (0.250) was only slightly less than the critical value of 0.265 at 20 df,$P < .10$ suggesting some minimal influence from marking.

Life Table

Estimates of total numbers of *L. d. disjunctus* in the study area passing through each of 12 life stages during 1983 were calculated (Table 13). Egg stage estimates are taken from the product of estimated adult females present in 1982 and the average number of eggs they were estimated to oviposit. This estimate is slightly less (17.7%) than the estimate derived from eggs hatched per unit area and area of bur reed present in September, 1982 (3,890,200). Use of the larger figure would reduce adult survival by approximately 3.0%.

Table 13. Estimated total number of *Lestes disjunctus disjunctus* in the study area entering each of twelve life stages in 1983.

Stage	Female	Male	Total
egg			3,202,000
I			730,800
II			723,800
III			713,700
IV			616,600
V			475,100
VI			419,800
VII			330,600
VIII	128,400	118,500	246,900
IX	81,000	74,700	155,700
X	66,800	61,700	128,500
adult	18,500	16,800	35,800

Sex ratio for instars VIII through X was determined to be 1.08:1.0 female to male. From the egg through instar VII a sex ratio of 1:1 was assumed.

Of 1,000 female eggs oviposited in 1982, an estimated 12 (1.2%) survived to the adult stage in 1983 (Table 14). Mortality was greatest in the egg stage when viewed in terms of numbers dying (d_x). However, q_x (proportion dying) was equally large in instar X (Table 14). Other mortality rates (q_x) tended to increase with increasing instars, with several exceptions. These exceptions were at instar V which was first collected on 9 June before emegration from the dead vegetation strata began and instar IX.

Mortality within the egg stage could be partitioned into three factors: overwintering mortality, mortality due to

Table 14. Life table parameters for female *Lestes disjunctus disjunctus* in the study area during 1983.

x	l_x	d_x	q_x	T_x	e_x	m_x
egg	1000	772	.772	1,937.0	1.94	
1	228	2	.009	1,323.0	5.80	
2	226	3	.013	1,096.0	4.85	
3	223	30	.134	871.5	3.91	
4	193	45	.233	663.5	3.44	
5	148	17	.115	493.0	3.33	
6	131	28	.214	353.5	2.70	
7	103	23	.223	236.5	2.30	
8	80	29	.362	145.0	1.81	
9	51	9	.176	79.5	1.56	
10	42	30	.714	33.0	0.79	
adult	12	12	1.000	6.0	0.50	45.2

$R_0 = (0.012)(45.2) = 0.542$

loss of vegetation containing eggs, and mortality at hatching (Table 15). The greatest source of explained mortality at the egg stage (18.9%) was due to loss of vegetation containing eggs. Egg mortality from overwintering (the difference in September 1982 and April 1983 estimates) was nearly as high as from vegetation loss, while mortality at hatching was relatively low.

Net reproductive effort calculated suggests that only slightly more than half the eggs this cohort began with will be replaced. Population rate of increase (λ), based on net reproductive rate was -0.612.

Evaluation of the influence of mortality factors on net reproductive effort was possible from calculation of

Table 15. Summary of mortality factors for female *Lestes disjunctus disjunctus* in the study area during 1983.

	Egg				Nymph	Adult
	Over- winter	Veg. Loss	Hatch- ing	Egg Total		
l_x				1000	228	12
d_x	167	189	6	772	216	12
% Apparent Mortality	16.7	18.9	6.0	77.2	94.7	12.0
% Indispensable Mortality	0.9	1.0	0.0	4.1	27.0	
log (Population size)				3.00	2.36	1.08

indispensible mortality (Table 15). This is the percentage of the population that would have survived to the adult stage had the mortality identified not occurred (Southwood 1978). Of the mortality factors quantified, vegetation loss and overwintering would have resulted in net reproductive effort increases to 0.994 and 0.949 respectively. Hatching mortality had a negligible effect on R_0.

DISCUSSION

Life History

In the St. Marys River *Lestes disjunctus disjunctus* is univoltine. It passes the winter in the egg stage, hatches the following spring, and completes nymphal development by early July. This life cycle is similar to life cycles previously reported for *L. d. disjunctus* from Saskatchewan (Sawchyn and Gillott 1974a) and Alberta (Baker and Clifford 1981). Overwintering in the egg stage is apparently common among Lestidae in north temperate climates, but rare among other Odonata (Corbet 1962). In western Canada, *L. congener* also overwinters in the egg stage (Sawchyn and Gillott 1974b). Of three species of Lestidae coexisting in a North Carolina pond, two (*L. d. australis* and *Archilestes grandis*) overwintered in the egg stage, while *L. vigilax* overwintered as early instars.

Eggs within stems of *Sparganium eurycarpum* collected in September and refrigerated 100 days at 1.0°C were successfully hatched. However, *S. eurycarpum* stems collected in September but not refrigerated failed to produce nymphs suggesting a temperature-controlled diapause. These observations are consistent with those of Ingram (1976) where *L. d. australis* eggs collected shortly after oviposition also failed to hatch but do not demonstrate diapause since diapause is set in the preceeding stage (adult in the present case). Sawchyn and Church (1973) studied L. d. disjunctus egg development in a a population from Saskatchewan. Eggs oviposited in July developed to near the point of hatching by late August, then entered diapause. Diapause development was initially controlled by temperature and later by photoperiod. Post-diapause development was also controlled by temperature and photoperiod, but could not take place unless eggs had been wetted. Sawchyn and Gillott (1974a) found that post-diapause development could take place at 0.0 °C and egg hatching could occur near 4.5 °C although such low temperatures would result in an extended hatching period. The estimated threshold temperature for L. d. disjunctus from the St. Marys River, 4.3 °C, is very near the minimum egg hatching temperature reported by Sawchyn and Gillott (1974a).

Nymphs first hatched from eggs in the study area on 14 May 1983. Hatching appeared to be at least moderately synchronized as maximum densities of first instar nymphs were collected on 18 May. Degree of hatching synchrony has not been investigated previously. However, diapause in the egg stage, combined with the rapid warming of water temperature in shallow littoral zones in north temperate areas, would suggest that synchrony of egg hatching may be a general phenomenon among Lestidae.

Nymphs of L. d. disjunctus developed rapidly through 10 instars in less than 60 days following hatching. Comparable developmental rates have been reported for other temperate zone Lestidae including: *L. d. disjunctus* in Canada (Sawchyn and Gillott 1974a; Baker and Clifford 1981), *L. disjunctus australis*, *L. vigilax*, and *A. grandis* in North Carolina, (Ingram 1976), *L. rectangularis* in Pennsylvania (Gower and Kormondy 1963), and *L. sponsa* in England (Corbet 1962).

The flight period of *L. d. disjunctus* from the St. Marys River is well within the range of time reported for the species in Canada (Walker 1953). Adults of *L. d. disjunctus* have been observed as early as 24 June in British Columbia and as late as 16 October in Saskatchewan (Walker 1953). In the present study *L. d. disjunctus* began emergence on 10 July 1983 and adults were last seen on 1 September. Most adults emerged during the first two weeks following initial emergence. This is consistant with well synchronized emergence of *L. d. disjunctus* reported from Saskatchewan by Sawchyn and Gillott (1974a). A similar pattern of emergence was noted in Saskatchewan for *L. unguiculatus* (Sawchyn and Gillott 1974a) and *L. congener* (Sawchyn and Gillott 1974b). In North Carolina Ingram (1976) found *L. d. australis*, *L. vigilax*, and *A. grandis* all had a more extended emergence period.

Most Lestidae exhibit a preference for a vegetation type to oviposit in although a variety of plant species may be available (Corbet 1962). Oviposition sites are also typically well above the water surface (Gower and Kormondy 1963; Bick and Hornuff 1966). In Saskatchewan, *L. d. disjunctus*, *L. unguiculatus*, and *L. dryas* all oviposited in green stems of *Scirpus* (Sawchyn and Gillott 1974a) while *L. congener* oviposited only in dry *Scirpus* stems (Sawchyn and Gillott 1974b). *Lestes disjunctus australis* has been reported to oviposit primarily in *Juncus* in North Carolina (Ingram 1976) and only in *Eleocharis* in Indiana (Bick and Bick 1961). In Indiana *L. eurinus* oviposited in *Sparganium americanus* and *L. unguiculatus* in *Sparganium* spp. (Bick and Hornuff 1966). In the St. Marys River *L. d. disjunctus* oviposited exclusively in green stems of *Sparganium eurycarpum*. Ovipositing in green stems may provide moisture necessary for pre-diapause development as suggested by Sawchyn and Gillott (1974a). However, selectivity of plant species for oviposition would not be necessary if moisture alone determined oviposition sites since many species of plants could provide moisture. It is possible that oviposition sites are also selected on the basis of the amount of cover that is provided for nymphs. Previous studies report nymphs favoring heavy cover. Walker (1953) noted that *L. d. disjunctus* inhabits areas rich in aquatic vegetation and Erickson (1984) found nymphs among *Glyceria* and *Carex* in a pond nearly filled with aquatic vegetation. In the St. Marys River in July 1983, the surface area of *S. eurycarpum* in a 1 meter plot in 0.5 m of water was over 7.5 m^2, three times the surface area provided by *Scirpus acutus* (2.5 m^2), the other common emergent macrophyte in the study area (Knoecklein pers. comm.). Dense emergent vegetation may be selected as oviposition sites to insure adequate cover for survival of offspring as well as providing moisture for eggs. Nymphs experience high mortality in the presence of fish and seek or are restricted to cover (Chapter Two).

Demographics

Studies of aquatic insect populations have generally not attempted to gather the kinds of data required for demographic analysis. Instead, researchers have focused on either the aquatic stages (Lawton 1970; Macan 1974; Benke and Benke 1975; Benke 1978) or aerial stages (Parr 1973; Garrison 1978; Garrison and Hafernik 1981) and only rarely on both. The only published data set sufficient to construct a complete survivorship curve was for Cordulia aernea amurensis, a species with a six year life cycle (Ubukata 1981). Ubukata (1981) estimated overall survival for this dragonfly from the egg through adult stage to be 0.17 to 0.20%. In the present study survival of L. d. disjunctus from the egg through the adult stage was estimated to be 1.20%. While survival of L. d. disjunctus is slightly greater than Ubukata reported, it is much shorter lived, being univoltine. Similarity in overall survival among species with such disparate life cycles may indicate mechanisms contributing substantially to mortality are intrinsic rather than environmental or that survivorship is more closely related to life history than seasonality.

A complete survivorship curve provides a summary of the proportion of a cohort surviving through time. Mortality occuring in specific stages or age classes which may influence life history characteristics are revealed by the shape of the curve. Animals from _Drosophila_ to man are remarkably similar in having survivorship curves which are varients of the diagonal or intermediate between type I and type II curves (Deevey 1947; Hutchinson 1978). In summarizing the available data for agricultural insect pests Price (1975) found species could be separated into two catagories based on the shape of survivorship curves. His type A species suffered 70% or greater mortality through mid-larval stages, while type B species experienced only 40% or less mortality through the same developmental stages. The survivorship curve for _L. d. disjunctus_ was intermediate between type A and B, but skewed toward the type B. However, mortality at the mid nymphal stage was also approximately 85%. This apparent anomaly arises from the comparison of cohort life table data with time specific life table data. Price's survivorship curves are plotted with instars on the x-axis and so are equivalent to time specific life table data whereas in the present study cohort life table for _L. d. disjunctus_ was developed.

Mortality in the egg stage was attributed to either loss of vegetation, overwintering, or difficulty at hatching. Mortality attributed to loss of vegetation was estimated to be the greatest single source of mortality in the egg stage, although mortality from overwintering was nearly as great. Since few studies of odonate populations have examined the egg stage and those studies dealt with ponds, comparable data from large open ecosystems are not available. This source of mortality was related to high water levels in combination with prevailing winds and commercial ship traffic which passes within 700 m of the study site. Water levels in the Great Lakes are variable. Average discharge in the St. Marys River during May has ranged from 1,331 to 3,443 $m^3 \cdot s^{-1}$ since control structures were constructed in 1922 (Quinn and Kelly 1983). When water levels are high in spring, plant stems broken off at the ice line are free to float up from the portion of the stem still attached to roots or rhizomes. Strong offshore winds during these periods of high water may serve to push floating stems offshore. Water displaced by passage of commercial vessels also generates water currents in littoral areas (Duffy et al. 1984) and may serve to export floating stems to offshore areas. The 6.0% mortality attributed to hatching difficulties is comparable to egg mortality reported for _L_. _d_. _disjunctus_ by Sawchyn and Church (1973). These authors found that egg mortality was related to temperature below freezing and varied from 6.0% at 0°C to 100% at -20.0 to -22.0°C. They found eggs deposited in stems located where snow collected experienced lower mortality than eggs deposited in stems which did not collect snow and this was attributed to the insulating properties of snow. Survival of _Enallagma_ _boreale_ nymphs frozen into ice in the

St. Marys River was also partially attributed to the insulating properties of snow (Duffy and Liston 1985). The portion of egg mortality attributed to freezing in the present study is well within the range reported by Sawchyn and Church (1973).

Survival of *L. disjunctus* during the entire nymphal period was 5.3%. This survival rate is similar to survival rates reported for *Ladona deplanata* (0.5-7.9%), *Epitheca* spp. (7.0-8.9%), and *Celithemis fasciata* (3.2-14.6%) in Georgia (Benke and Benke 1975). Lawton (1970) found survival of *Pyrrhosoma nymphula* varied from 0.5 to 30.0 or 40.0% among cohorts. Macan (1964) reported 50.0% survival in *Enallagma cyathigerum* , considerably higher than survival of *Pyrrhosoma nymphula* from the same pond.

Sources of mortality in nymphal stages were not determined. Dietary analysis of predators (*Aeshna canadensis*, *Libellula* spp. (Anisoptera), red-spotted newt (*Notophthanlmus viridescens viridescens*), juvenile brown bullhead (*Ictalurus nebulosus*), juvenile bluegill (*Lepomis macrochirus*), and juvenile rock bass (*Ambloplites rupestris*)) from the study area revealed low numbers of damselfly nymphs with none being identified as Lestidae (Day 1983; Duffy unpublished). In other areas of the St. Marys River, Odonata occurred in 62.5% of stomachs from juvenile rock bass 76 - 115 mm (Green 1980). While Green (1980) found no Lestidae in fish he examined, his fish were collected from beaches and areas of low cover where Lestidae would probably not occur.

Relatively low numbers of this size rock bass were found in the study area, however, low numbers of a vertebrate predator such as this could inflict heavy mortality on an odonate population. Other predators common in the study area which may have preyed on nymphs include *Ranatra* spp., *Lethocerus americanus*, and *Belostoma* spp. Each of these invertebrate predators occurs in heavy vegetation, which would place them in proximity to *L. d. disjunctus* nymphs.

Studies of adult odonate populations have apparently been limited to pond environments (Corbet 1980). Maximum numbers of adults associated with ponds typically range from less than 100 to over 1,000 (Corbet 1952; Moore 1964; Parr 1973, 1976; Van Noordwijk 1978; Garrison 1978; Garrison and Hafernik 1981; Ubukata 1981). Maximum population size for *L. d. disjunctus* in 1983 was approximately an order of magnitude greater than has previously reported. Recapture rates in the present study were lower than rates often reported for pond studies and probably overestimated population estimates somewhat. Garrison and Hafernik (1981) were able to recapture 73% of *Ischnura gemina* marked around a small seepage in California. Ubukata (1981) recaptured 50% of the 22 dragonflies he marked and Garrison (1978) 23% of the damselflies he marked. In addition, some emigration from the study area was detected in the current study. Emmigration from the study area would also result in overestimates of population size.

The number of eggs carried by Odonata varies widely among species. Endophytic species, which place eggs inside plant tissues, in general lay fewer eggs than exophytic species which lay eggs in water. Most Zygoptera oviposit endophytically. Among Zygoptera, Calyopteryx maculata may lay from 1,267 to 1,810 eggs over a 4 to 14 day period and from 525 to 750 per day (Waage 1978). Sawchyn and Gillott (1974a) found that L. d. disjunctus in Saskatchewan laid only 6 eggs per episode. They found 45 and 112 eggs in two females examined and suggested the latter number was a probable fecundity value. Their total egg counts, although limited, is in close agreement with egg counts for females from the St. Marys River.

Net reproductive effort calculated from data on potential fecundity and adult population size was 0.542 (λ = -0.612) indicating the present cohort would replace only slightly more than half of the eggs from which it arose. Had eggs not been lost from the population with vegetation that was carried offshore prior to egg hatching, net reproductive effort would have been 0.994 (λ = -0.006) and the present cohort would have been capable of replacing itself or nearly so. Since seasonal flows in the St. Marys River appear to be stochastic with periods between high water years ranging from 2 to 14 years since 1900 (Quinn and Kelly 1983) it is unlikely that L. d. disjunctus has evolved to compensate for this source of mortality.

CHAPTER TWO

The Influence of Environmental and Biological Factors on Growth, Survival and Habitat Selection in *Lestes disjunctus disjunctus*

INTRODUCTION

Odonata are common predatory aquatic insects of freshwater lentic littoral zones and, in favorable environments, often coexist in diverse assemblages comprising a relatively large proportion of the total invertebrate biomass where they occur (Corbet 1962, 1980; Benke and Benke 1975; Crowder and Cooper 1982; Crowley and Johnson 1982). These factors, along with the relatively long odonate nymphal period have prompted considerable interest in the mechanisms which influence growth, survival, and facilitate coexistance among species (Lawton et al. 1980; Johnson et al. 1985). Since the pond and lake littoral environments in which odonates attain greatest density and diversity are physically and biologically complex, it seems plausible that both physical factors and interactions with other predators would influence growth and survival (Benke 1978; Crowder and Cooper 1982; Wetzel 1983).

The thermal regimes of north temperate littoral zones fluctuate on both a diel and annual cycle in response to fluctuations in air temperature (Ward and Stanford 1982). This heterogeneous thermal environment enables a greater array of species to inhabit littoral zones than inhabit more thermally stable environments, by providing a wider range of temperatures (Sweeney and Vannote 1978; Vannote and Sweeney

1980). In aquatic insects typically inhabiting littoral zones, growth and development is positively related to increasing water temperature (Mackay 1979; Merritt et al. 1982). Water temperature influences the physiology of potential prey and prey capture rates as well as the physiology of the odonate (Bottrell et al. 1976; Cresens et al. 1982; Erickson 1984). The diet of odonate nymphs consists primarily of microcrustacea and chironomid larvae which appear to be a high quality food resource (Vijverberg and Frank 1976). Furthermore, these prey are typically common at water temperatures favorable for odonate growth, suggesting that food limitation under natural conditions is unlikely (Bottrell et al. 1976). However, interactions with other odonates, other predaceous insects, or fish may depress prey capture rates, influencing growth and survival.

Lestes disjunctus disjunctus inhabits permanent ponds, marshy bays, and slow weedy streams throughout Canada and the northern United States (Walker 1953). In the St. Marys River, Michigan *L. d. disjunctus* hatches in spring and develops rapidly, with emergence occurring in early July. Experiments reported here were conducted to elucidate mechanisms influencing growth and survival of *L. d disjunctus* and to aid in the understanding of demographic data reported in Chapter one. Three questions were posed in designing experiments: 1) what is the influence of water temperature and prey density on growth and survival of nymphs? 2) what influence do naturally coexisting predators have on the growth and survival of *L. d. disjunctus*? 3) what influence do fish have on habitat selection and survival? *A priori* hypotheses were that increased growth and survival rates would be positively correlated with higher water temperatures, higher prey densities, and lower coexisting predator levels. For the fish - habitat experiment,the hypothesis was that fish would restrict the distribution of nymphs to heavy cover and increase nymph mortalitiy rates.

MATERIALS AND METHODS

Water Temperature-Prey Density

The influence of water temperature and prey density on growth and survival of L. d. disjunctus nymphs was studied under controlled conditions. Nymphs used for the experiment were obtained from eggs collected in the study area and hatched at treatment temperatures. Hatching was completed on 23 May, the experiment begun on 24 May, and continued through 26 July 1983.

An experimental design consisting of rearing nymphs in low, medium, or high prey density microcosms at both 16 or 20°C was employed throughout the experiment. Duplicate microcosoms were employed at each prey level and water temperature combination. Low, medium, and high prey densities were defined as 0.5, 1.0, and 2.0 times the density of prey in the field study area at the time prey in microcosms were replenished. Thus, prey density in microcosms was allowed to vary during the course of the experiment while tracking prey resources in the environment.

Microcosms used were 30 x 45 x 10cm deep plastic commercial bus trays filled with 5 liters of river water filtered through a 149μ sieve. Water temperature was controlled by floating microcosms in a "Living Stream" used as a water bath. Each microcosm was stocked with 20 first and/or second instars. This stocking level equaled 140 nymphs$\cdot$m^{-2}, similar to peak densities recorded in the field.

Prey were replenished with natural prey from the study area (149 600μ microcrustacea, oligocheates, and chironomid larvae) and microcosm water completely exchanged with filtered river water at 3 day intervals. Every 3 days, 70 liters of river water was collected from the study area using plastic pails and concentrated to 10 liters through a 149μ sieve. The 60 liters of filtered water was used to change microcosm water. The 10 liters containing prey was passed through a 600μ sieve to remove large invertebrates, mixed, and 1.0, 0.5, and 0.25 liters added to high, medium, and low prey microcosms respectively.

Survival was monitored weekly by counting all nymphs remaining in microcosms. Growth, determined by measuring the length of 10 nymphs in each prey density and temperature treatment, was also monitored weekly. Length measurements, excluding caudal lamella, were recorded to the nearest 0.1 mm under a stereozoom binocular microscope equipped with an ocular micrometer. When measuring nymphs, small individuals were transferred from microcosms to petri dishes containing water using a "turkey baster", larger individuals were transferred using an aquarium net. Nymphs did not appear stressed by this procedure. Length data was later converted to dry weight using a length-dry weight regression equation developed for _L_. _d_. _disjunctus_. Toward the end of the experiment, fewer than 10 nymphs remained in some treatments. Specific growth rate was determined at each water temperature and prey level using the equation (Sweeney and Schnack 1977):

$$GR = (\ell\eta W_{t2} - \ell\eta W_{t1})/T$$

where $\ell\eta$ = natural logarithm; GR = instantaneous growth rate; W = dry mass; and T = time interval. Specific growth rate at each temperature was then expressed as a function of prey density using the Michaelis-Menten equation:

$$\mu = \mu_{max}(P/K_p + P)$$

where μ is specific growth rate; μ_{max} = maximum specific growth rate; P = prey density level; and K_p = prey density at 0.5 μ_{max}.

Growth response and survival among water temperature and prey density treatments was also tested using separate two-way ANOVA of final dry mass and of average mortality/day. This provided a statistical measure of significance in differences observed.

Competition - Predation

The influence of competition on growth and survival of L. d. disjunctus was studied by rearing nymphs in the presence of other predators with which it naturally occurs. These other predators were collected from the study area and included Enallagma hageni, Aeshna canadensis, Buenoa spp., and Umbra limi. Aeshna canadensis, Buenoa spp., and U. limi hatch in spring at about the same time as L. d. disjunctus . Enallagma hageni overwinter as nymphs in mid-instar.

Competition experiments were conducted in 1.0m diameter plastic wading pools each having an area of 0.78m^2. Each pool was filled with 100 liters of filtered river water and covered with a mat of dead *Sparganium eurycarpum* stems to simulate conditions in the study area where nymphs hatch and co-occur with the potential competitors used. Stems had been dried prior to adding them to pools to eliminate hatching of either *L. d. disjunctus* or other animals and contaminating experiments. Stocking rates were chosen to reflect conditions observed in the field. All pools were stocked with 100 *L. d. disjunctus* nymphs (= $128 \cdot m^{-2}$). Four pools weredesignated as treatment pools with pool one receiving 10 *E. hageni*; pool two, 15 *A. canadensis*; pool three, 15 *Buenoa* spp.; pool four, 20 *U. limi*; and pool five, the control pool, receiving no additional stocking.

Each week 20% of pool water was exchanged with filtered river water and prey coollected from 40 liters of river water were added to each pool. Algal and microinvertebrate communities developed in pools within two weeks and all appeared similar. Water temperature was measured and pools examined for possible invading animals daily.

Growth and survival of nymphs in pools was measured weekly. Growth was determined by measuring the length of 10 nymphs from each pool, then converting length data to dry mass as in the temperature-prey experiment. Survival was estimated by sampling, since pools were designed to simulate natural conditions and cover added prevented counting all nymphs present. Weekly sampling consisted of triplicate sweep samples in each pool using a 15cm wide rectangular aquaria net. A single sweep sample represented 600cm^2 or 7.6% of the pool area and was collected by placing the net in the center of the pool and pushing it to the outer edge. At the termination of experiments regular sampling was conducted, then pools drained and all nymphs couted to assess the efficiency of sampling.

Data for growth and survival were analyzed using one-way ANOVA. Growth was measured as final dry mass and survival as average mortality per day.

Habitat Selection

Field observations suggested distribution of L. d. disjunctus nymphs is limited to areas of heavy cover. To quantify the influence of fish on habitat selection and survival, an experiment was designed in which nymphs were exposed to three cover densities first without, then with fish.

Habitat selection experiments were conducted in a 100 liter fiberglass aquarium measuring 70 x 50 x 30cm deep fitted with an under gravel filter. Washed sand and gravel substrate was added and aquatic macrophytes planted to achieve three cover levels. Each cover level occupied one third (1,165cm^2) of the aquarium. Macrophytes planted included 2 clumps of Carex spp. and 2 Ranunculus spp. to provide heavy and medium cover respectively. Low cover consisted of floating dead Scirpus spp. stems which covered less than half of the low cover surface area. Following planting, the aquarium was allowed to equilibrate for 1 week. At the end of the week, 20 late instar (VI - VIII) nymphs were introduced and allowed to acclimate 3 days before experiments were initiated.

Following the acclimation period habitat selection by nymphs was recorded for 5 consecutive days. Data recorded during the experiment included the number and position of nymphs in each of the three cover areas at dawn, mid-day, and dusk. Positions recorded included the aquarium bottom, side, and on plants. After 5 days, three bluegill sunfish (Lepomis macrochirus) 48 to 60 mm total length were introduced and the 5 day experiment repeated. Data were analized using a three-level nested ANOVA.

Field Data

Growth under natural conditions was investigated for a population of L. d disjunctus inhabiting the St. Marys River. Nymphs were collected weekly for the purpose of obtaining dry weight data from which a length-weight relationship could be determined. Following collection, nymphs were returned to the laboratory and held in aquaria containing filtered water for 24 hours to insure passage of fecal pellets. Total length, excluding caudal lamellae, was then recorded to the nearest 0.1mm under a binocular microscope equipped with an ocular micrometer. Length was recorded and nymphs placed in pre-weighed pans, oven dried at 60°C for 48 hours, moved to a dessicator containing $CaSO_4$ until cooled, then weighed to to the nearest 0.1mg using a Mettler M1500 balance. Data recorded were used to calculate a regression equation relating dry weight to length.

A detailed demographic study of L. d. disjunctus in the St. Marys River conducted during 1983 provided length measurements for all instars as well as survival estimates and distributional data. A complete description of field methods and discussion of results is presented in Chapter One.

RESULTS

Length-Dry Weight

A length-dry weight relationship was developed from measurements of 179 nymphs (Figure 9). Lengths measured ranged from 2.2 to 21.1mm, while dry weight ranged from 0.1 to 12.6mg. Dry weight was related to length for individual nymphs by the exponential regression equation:

$$\ell\eta W = \ell\eta 0.12 + 0.22(L),\ r^2 = 0.97$$

where $\ell\eta$ = natural logarithm; W = mg dry weight; and L = mm length excluding caudal lamellae.

Water Temperature-Prey Density

Growth of nymphs as determined by final dry weight was significantly greater at 20°C than at 16°C [$F_{(1,4)} = 31.88$, $P < .005$]. Nymphs in 20°C treatments averaged 4.55, 5.43, and 5.20mg after 64 days for low, medium, and high prey levels respectively while nymphs in 16°C treatments averaged 1.18, 2.11, and 2.05mg for the same prey levels (Figures 10, 11, and 12). Average final dry weight of nymphs at 20°C was 199% greater than final dry weight at 16°C over all prey levels.

No significant difference was found in growth among prey levels [$F_{(4,37)} = 2.34$, $P > .05$]. Growth at the medium prey level was greatest for both temperature treatments (Figures 10, 11, and 12). Evidence of physical attack was also

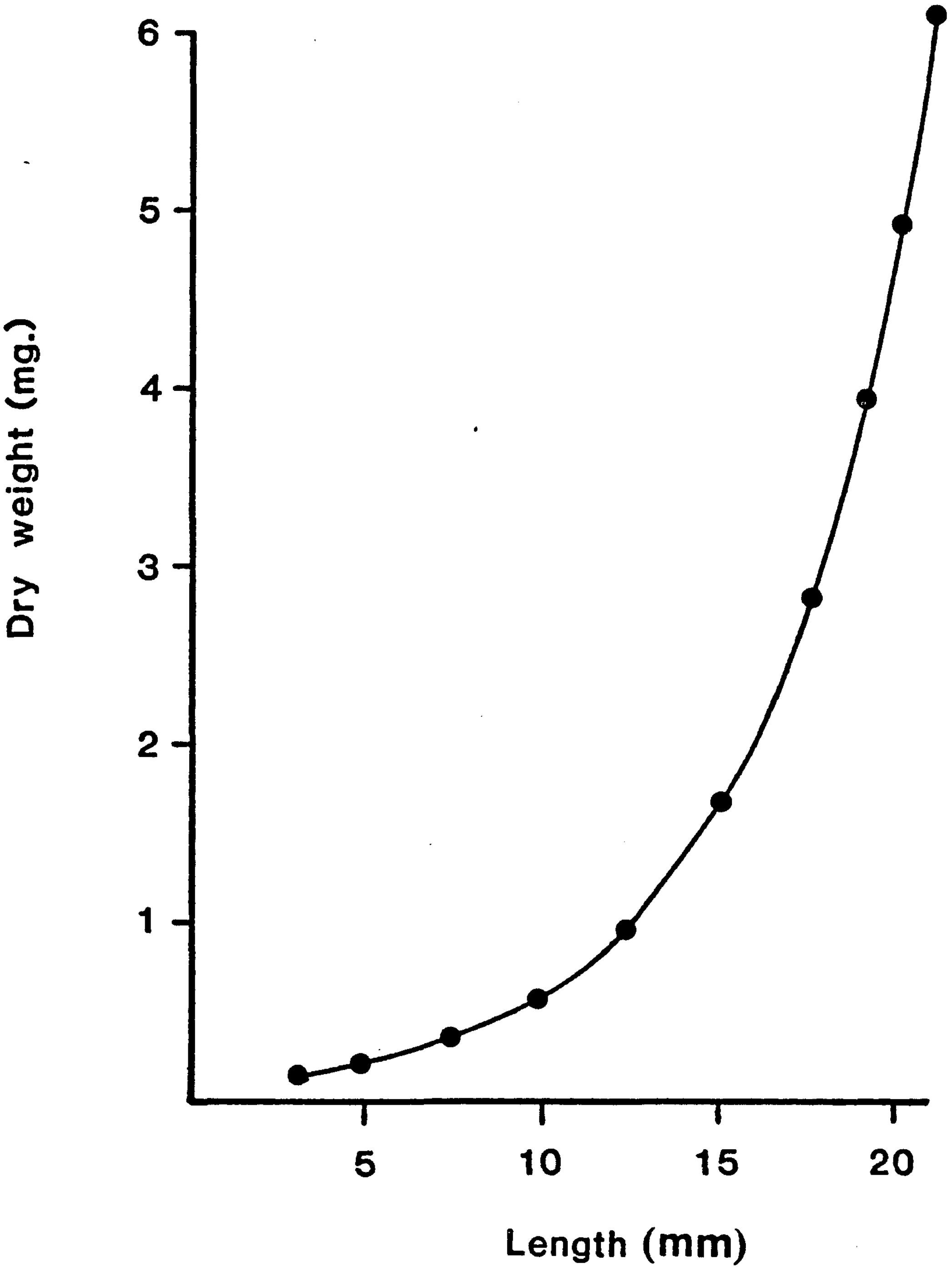

Figure 9. Length-dry weight relationship for *Lestes disjunctus disjunctus* nymphs from the St. Marys River. Curve fitted by regression.

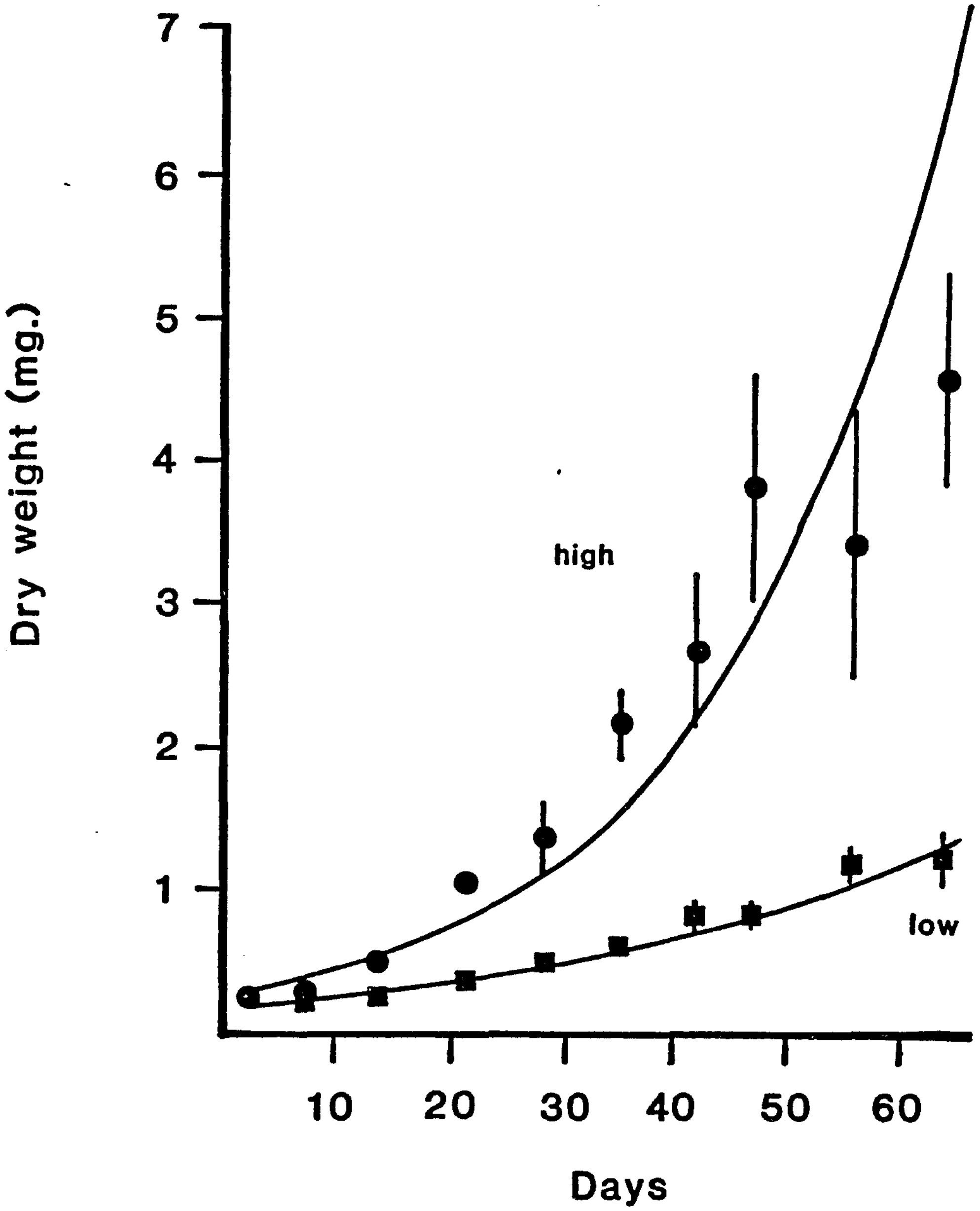

Figure 10. Growth of <u>Lestes</u> <u>disjunctus</u> <u>disjunctus</u> at 16 and 20°C in low prey microcosms. Data are plotted as means and standard errors with a line fitted by regression.

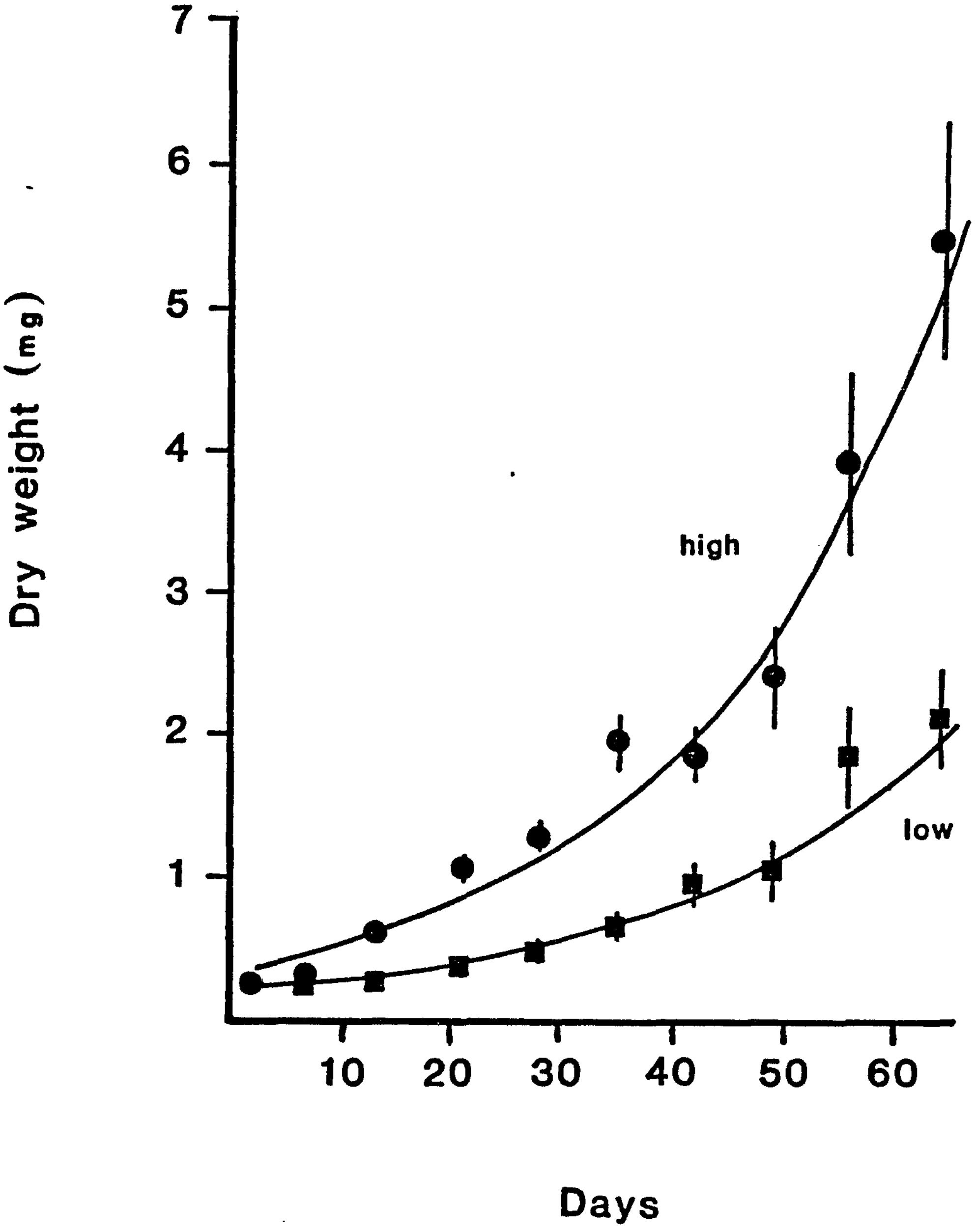

Figure 11. Growth of *Lestes disjunctus disjunctus* at 16 and 20°C in medium prey microcosoms. Data are plotted as means and standard errors with a line fitted by regression.

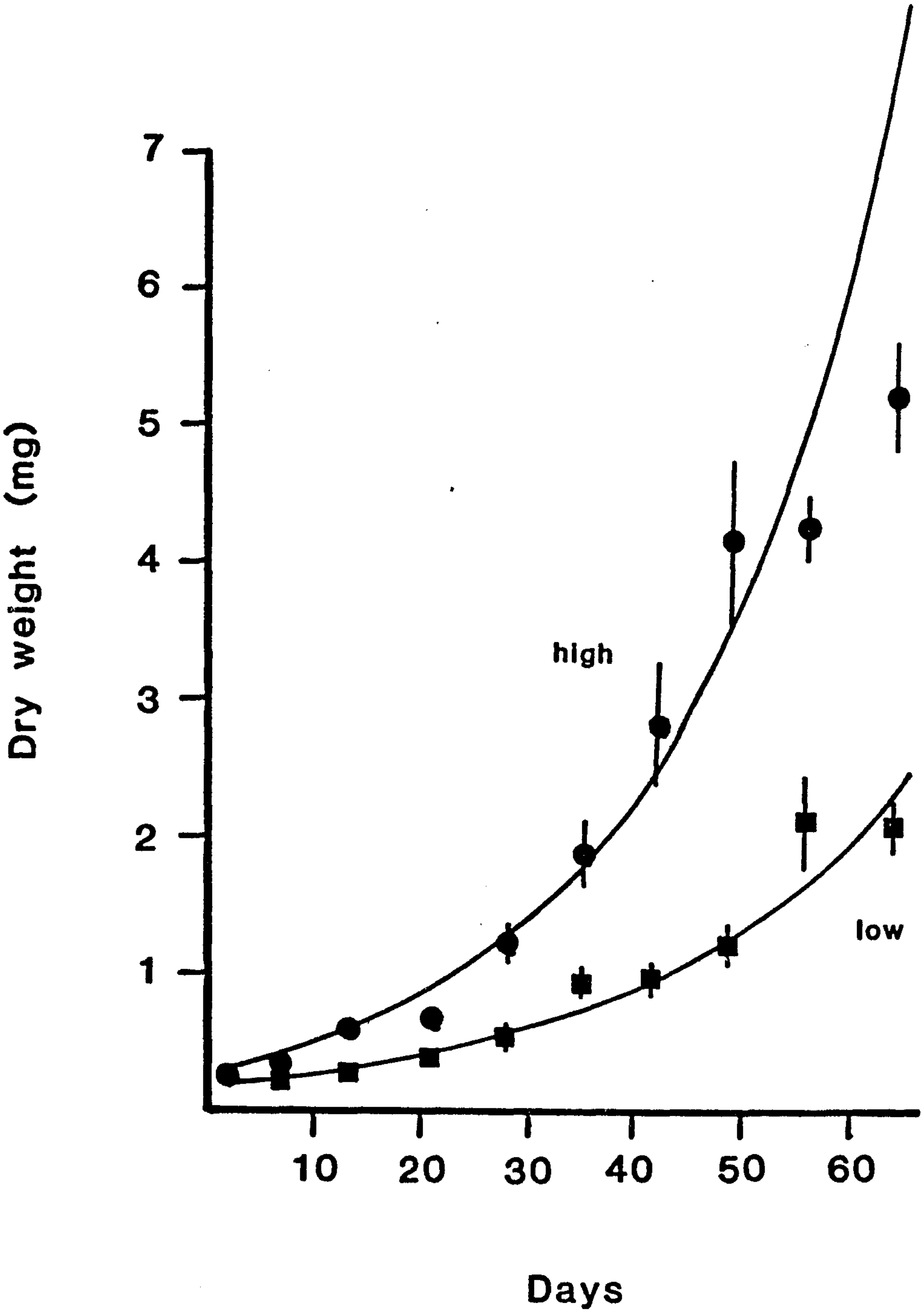

Figure 12. Growth of *Lestes disjunctus disjunctus* at 16 and 20°C in high prey microcosms. Data are plotted as means and standard errors with a line fitted by regression.

greatest at medium prey levels. This evidence included missing lamellae on live nymphs and partially canabalized dead individuals.

Instantaneous growth rates (equivalent to % growth per day) at 20°C averaged .055, .060, and .065 for low, medium, and high prey levels while instantaneous growth rates at 16°C were .030, .037, and .039 for the same prey levels. Regressing (prey level/ instant- aneous growth rate) against instantaneous growth rate yielded a half saturation (K_p) prey value of 0.179 and maximum specific growth rate (μ_{max}) of 0.70 for 20°C ($r^2 = .94$). Half saturation and maximum specific growth rate (μ_{max}) values for 16°C were 0.161 and 0.39 respectively ($r^2 = .67$). Prey specific growth rates calculated from these data produce curves nearing an asymptote at the high prey level for both temperatures where they bracket average specific growth (0.061) of nymphs in the field (Figure 13).

Nymphs in high prey microcosms had significantly greater survival than nymphs in either medium or low prey microcosms [ANOVA, $F_{(2,6)} = 19.85$, $P < .005$]. Overall survival after 64 days was greater at 16°C than at 20°C (Figures 14 and 15). However, differences among temperature treatments were not significant [ANOVA, $F_{(1,6)} = 2.81$, $P > .05$].

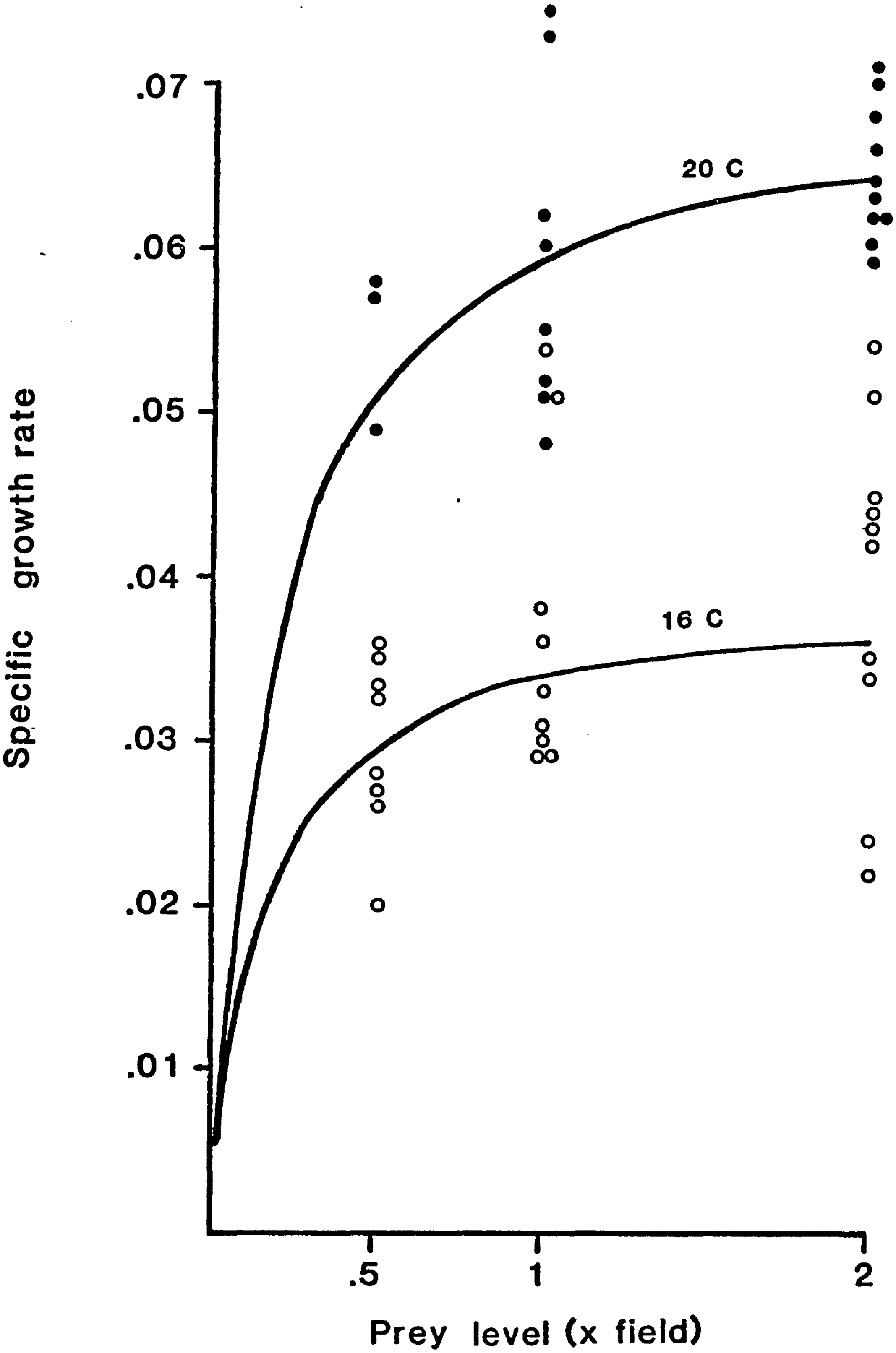

Figure 13. Specific growth rate of Lestes disjunctus disjunctus at 16 and 20°C as a function of prey level. Curves fitted by specific growth equation.

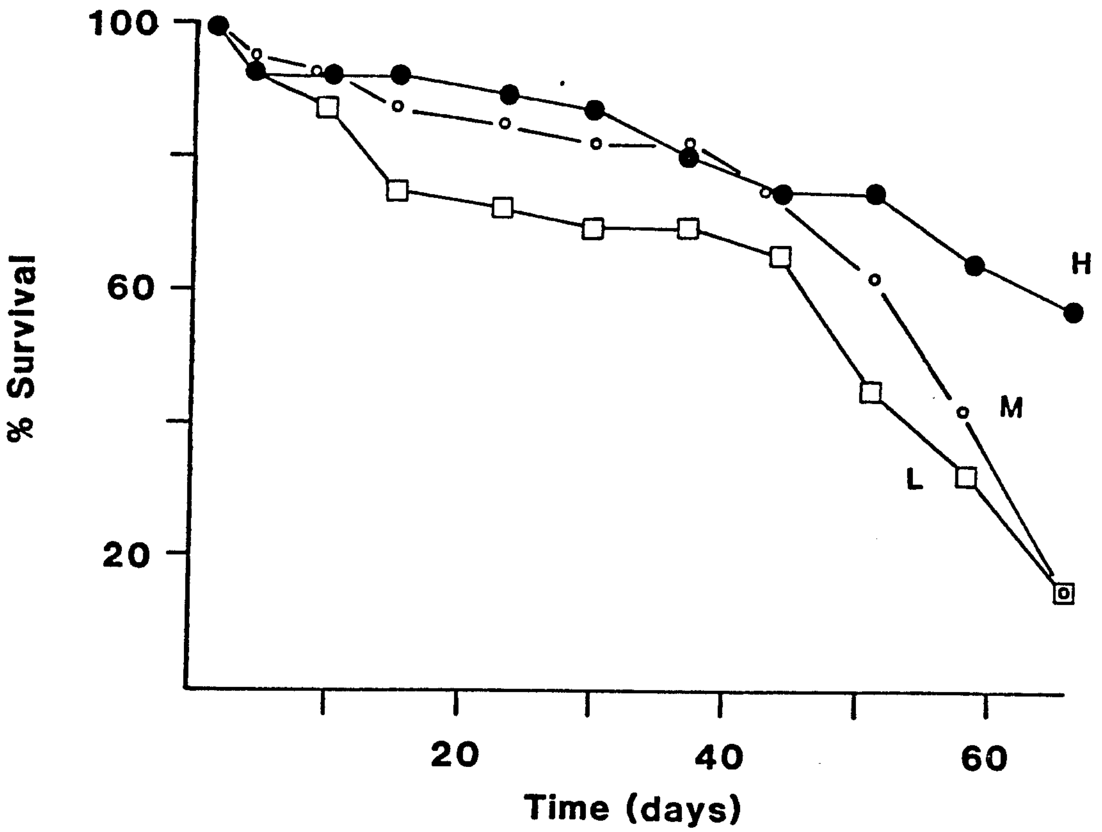

Figure 14. Survival of Lestes disjunctus disjunctus in high, medium, and low prey microcosms at 16°C.

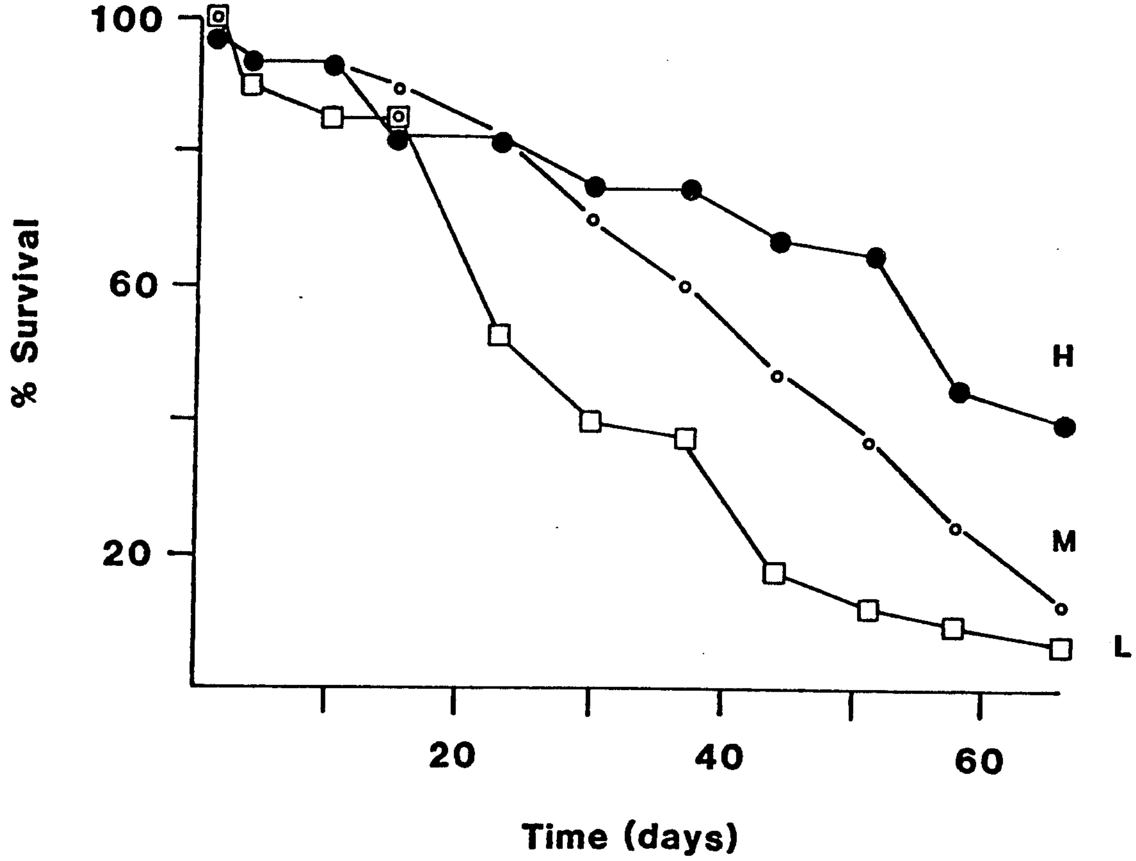

Figure 15. Survival of Lestes disjunctus disjunctus in high, medium, and low prey microcosms at 20°C.

Competition-Predation

Competition experiments were terminated following day 51 as emergence of L. d. disjunctus from several pools began prior to day 58 sampling. Water temperature in pools varied with littoral zone temperatures but were slightly warmer (Figures 5 and 16). No significant differences in growth among control or treatment pools could be detected after 51 days [ANOVA, $F_{(4,28)} = 0.97$, $P > .25$] (Figure 17). Instantaneous growth rates for L. d. disjunctus ranged from 0.052 to 0.070 while instantaneous growth rates for other predators ranged from 0.026 to 0.101 (Table 16).

Pool samples underestimated nymph density in most cases (Table 17). Differences among estimated and actual density were significant ($X^2_{v4} = 12.58$, $P < 0.05$). Survival of L. d. disjunctus was influenced by the of presence A.canadensis and probabley E hageni (Figures 18 and 19). Survival was significantly lower in the A. canadensis treatment pool than in other pools [$F_{(4,10)} = 9.65$, $P < .005$, SNK test]. Differences in survival among all other pools were not significant. Nymphs in E. hageni pools experienced high mortality during the initial two weeks of experiments, however, E. hageni began to emerge from pools during the third week releasing L. d. disjunctus from competition or predation. Survivorship curves for all other treatments were similar.

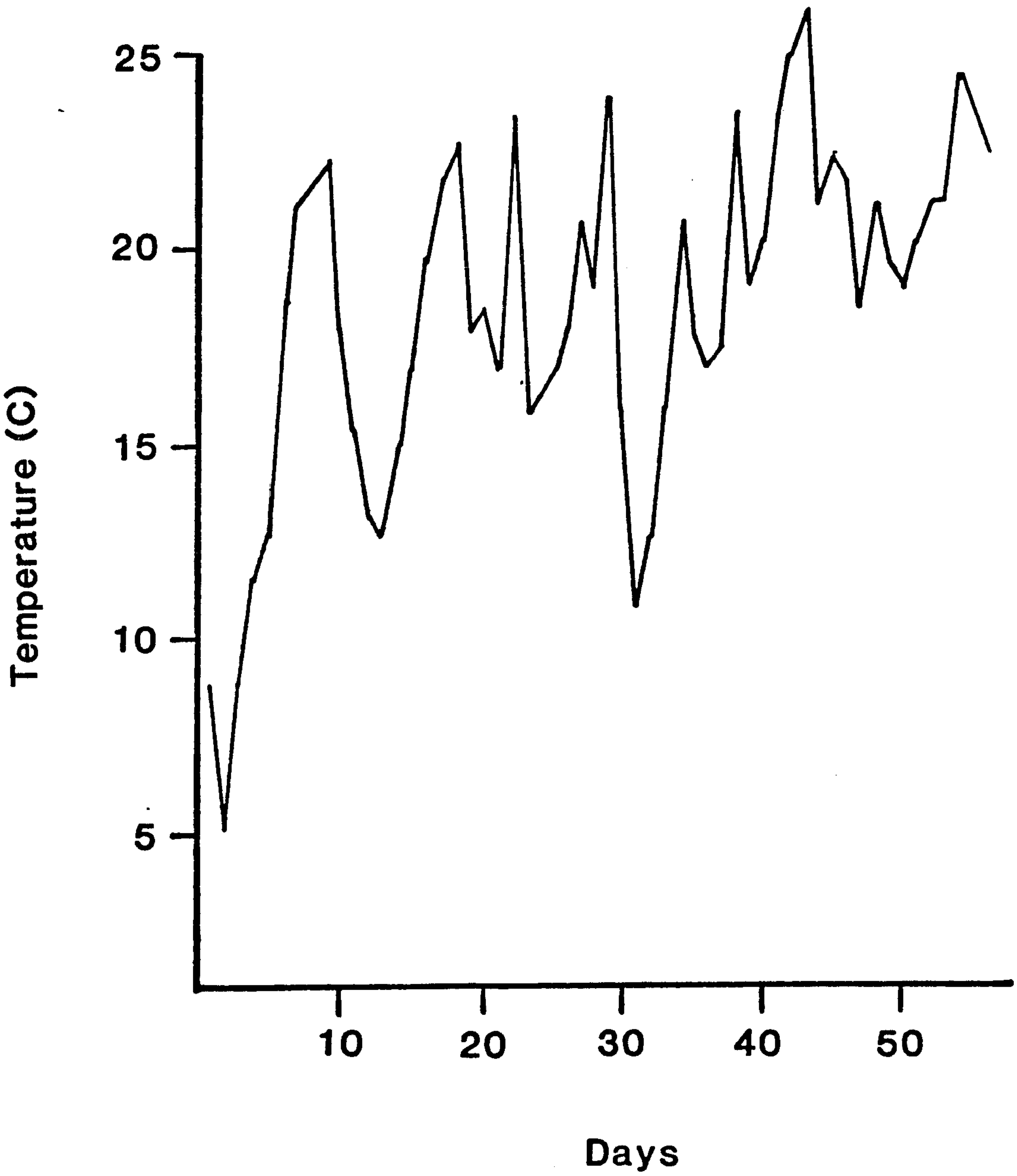

Figure 16. Average daily water temperature recorded in experimental pools during competition experiments.

Table 16. Instantaneous growth rates of *Lestes disjunctus disjunctus* , other invertebrate, and a vetebrate predator in competition-experiment pools.

	Competitor				*L. d. disjunctus*			
	W_i	W_f	GR	Days	W_i	W_f	GR	Days
Control					.31	4.87	.054	51
A. canadensis	.4	12.2	.101	44	.26	5.58	.070	44
E. hageni	2.0	5.2	.042	22	.31	5.13	.056	51
U. limi	.9	2.9	.023	51	.32	4.56	.052	51
Buenoa spp.	.4	1.5	.026	51	.27	5.78	.060	51

Table 17. Comparison of estimated number of *Lestes disjunctus disjunctus* in competition-predation pools from sampling on the final day of experiments with the actual number recovered.

	Number/m^2	
Treatment	Estimated	Actual
Control	33	23
A. canadensis	0	4
E. hageni	11	13
Buenoa spp.	22	28
U. limi	28	38

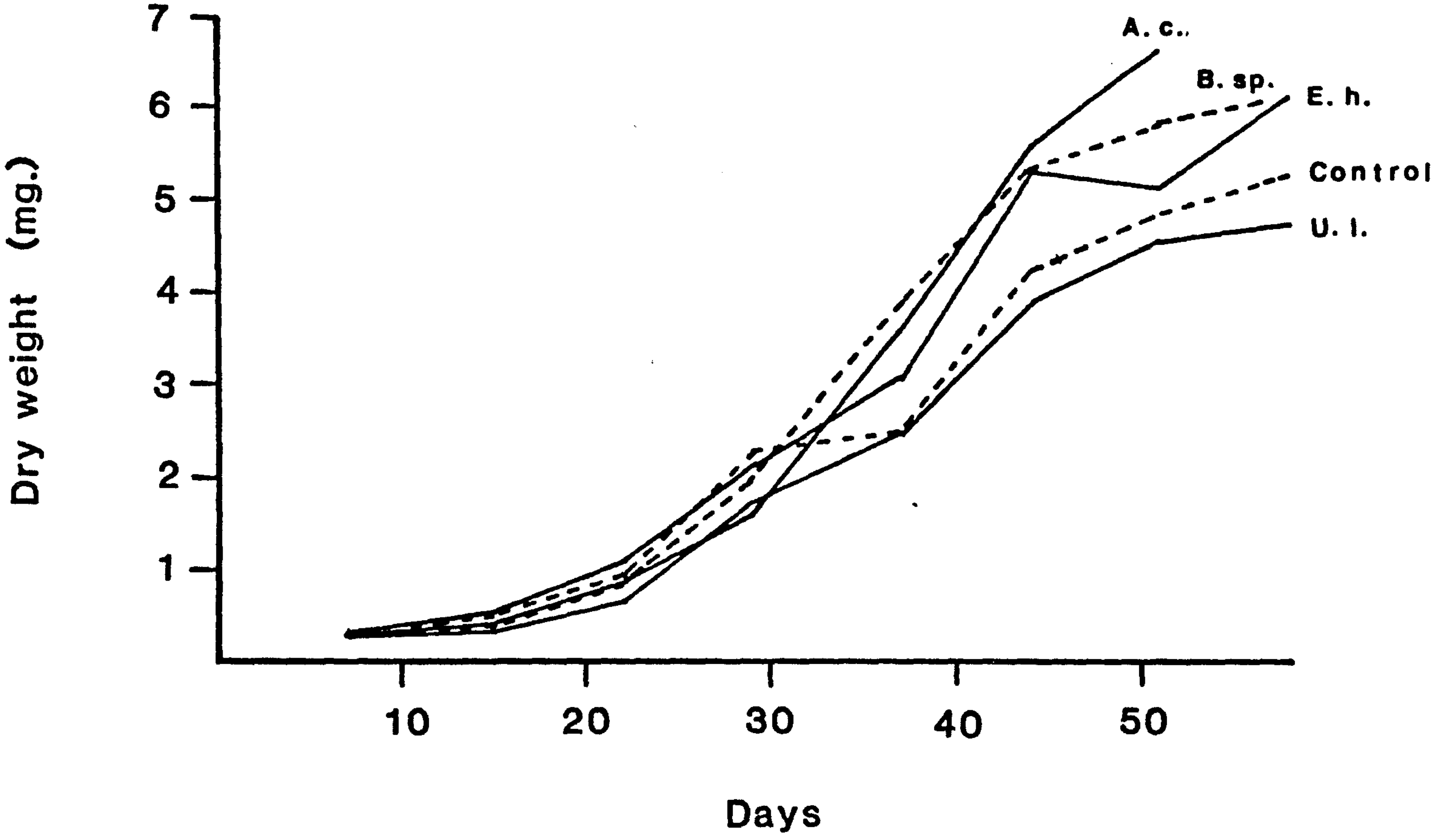

Figure 17. Growth of *Lestes disjunctus disjunctus* in the control pool and in pools with *A. canadensis*, *E. hageni*, *Buenoa* spp., or *U. limi* pools.

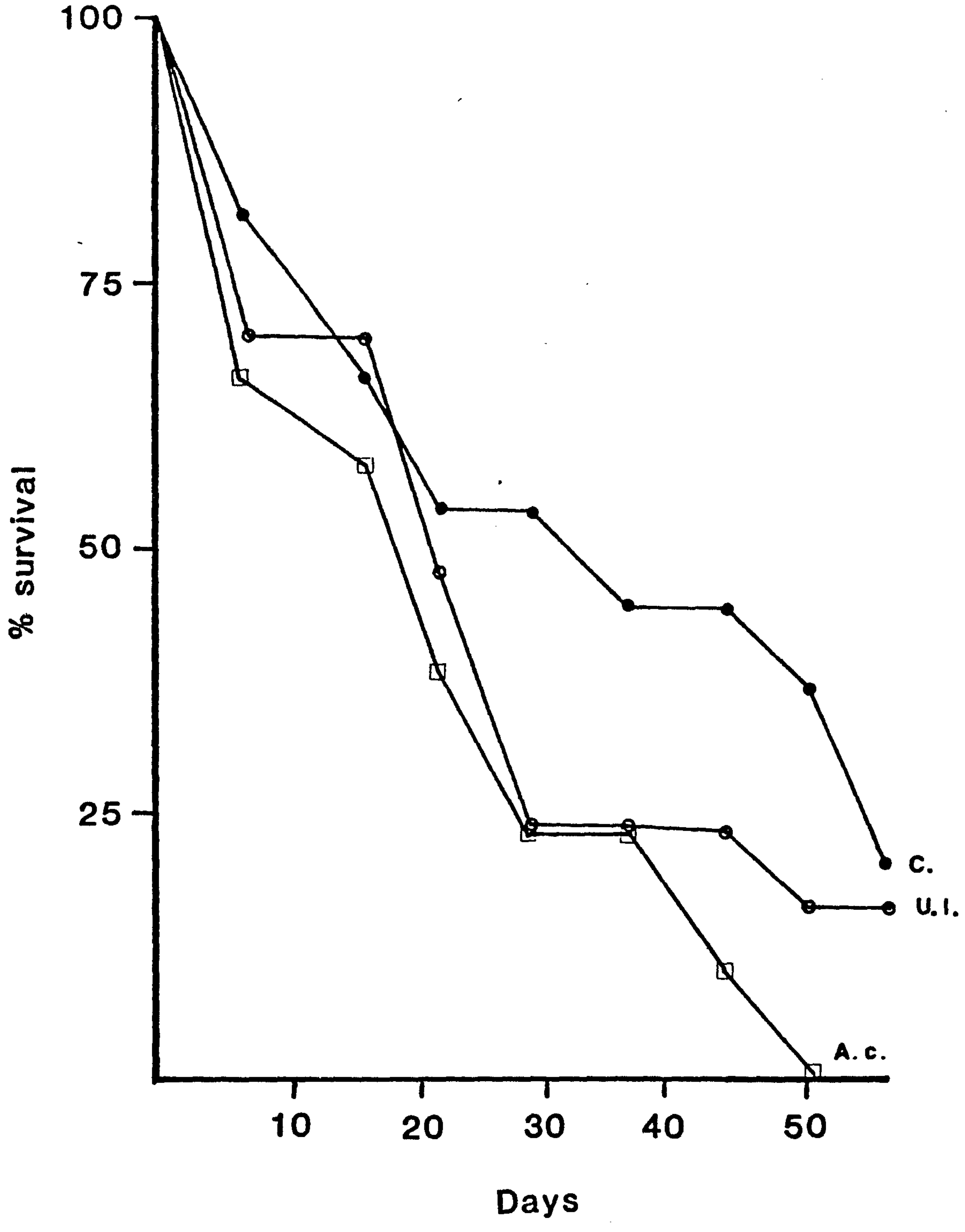

Figure 18. Survival of *Lestes disjunctus disjunctus* in the control pool and in pools with *Umbra limi*, or *Aeshna canadensis*.

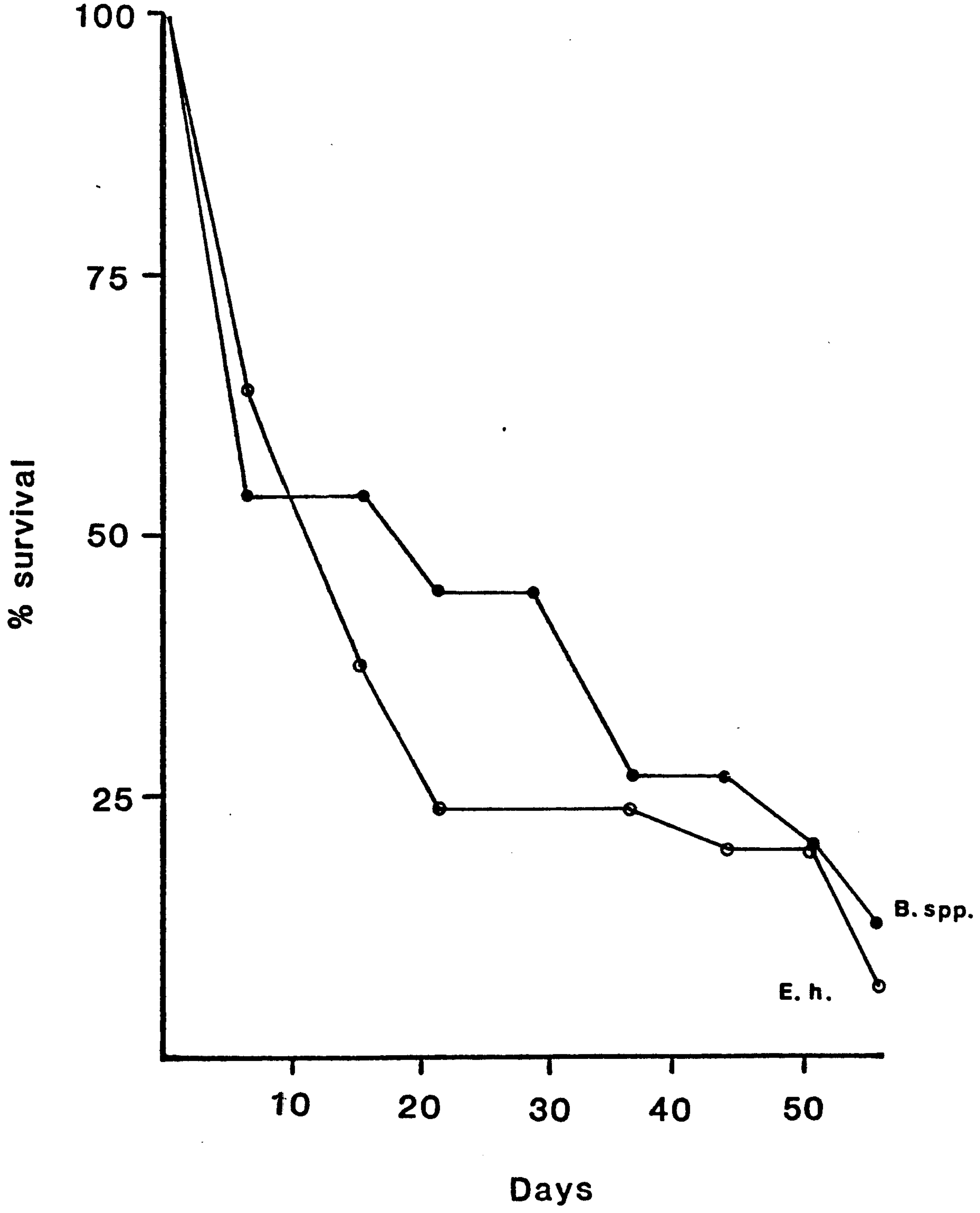

Figure 19. Survival of Lestes disjunctus disjunctus in the Buenoa spp. and Enallagma hageni treatment pools.

Habitat Selection

The presence of fish had an influence on both the survival and habitat selection of L. d. disjunctus nymphs (Figure 20). Average number of nymphs per observation period in the absence of fish (18.7) was significantly greater than after (11.0) fish had been introduced [$F_{(1,4)} = 141.76$, $P < .001$].

Nymphs in aquaria without fish occurred in cover density types and areas within cover equally excepting dead stems in low cover (Figure 20). Nymphs in the fish treatment also selected cover types approximately equally, however, in the presence of fish, nymphs were much more abundant on plants in all cover densities(low cover density plants were dead stems). Differences in distribution were greatest in low cover and least in the high cover area and differences in nymph density among cover types were significant [$F_{(12,162)} = 21.67$, $P < .001$).

Field-Laboratory Comparisons

Survival of nymphs reared at 20°C and high prey density, and nymphs in the control pool from competition-predation experiments was compared with survival of nymphs in the field. Survival of nymphs in the control pool after 51 days was 18.0% and was similar to the 18.6% survival observed in the field population at day 53 (Figure 21). Nymphs reared at 20°C and high prey density exhibited higher survival rates than in either the control pool or field (Figure 21).

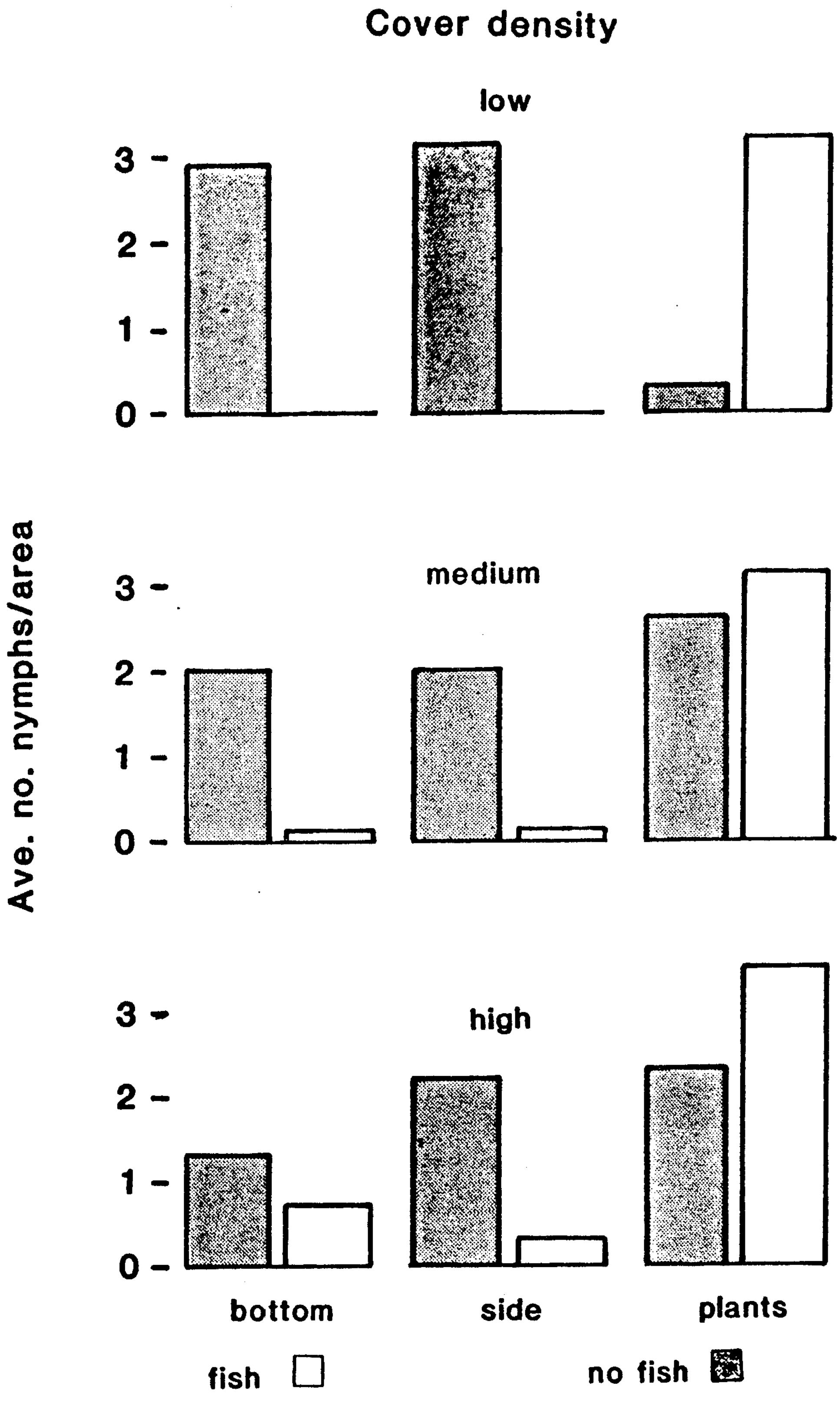

Figure 20. Average number of Lestes disjunctus disjunctus nymphs in three cover areas and three cover densities with and without Lepomis macrochirus present.

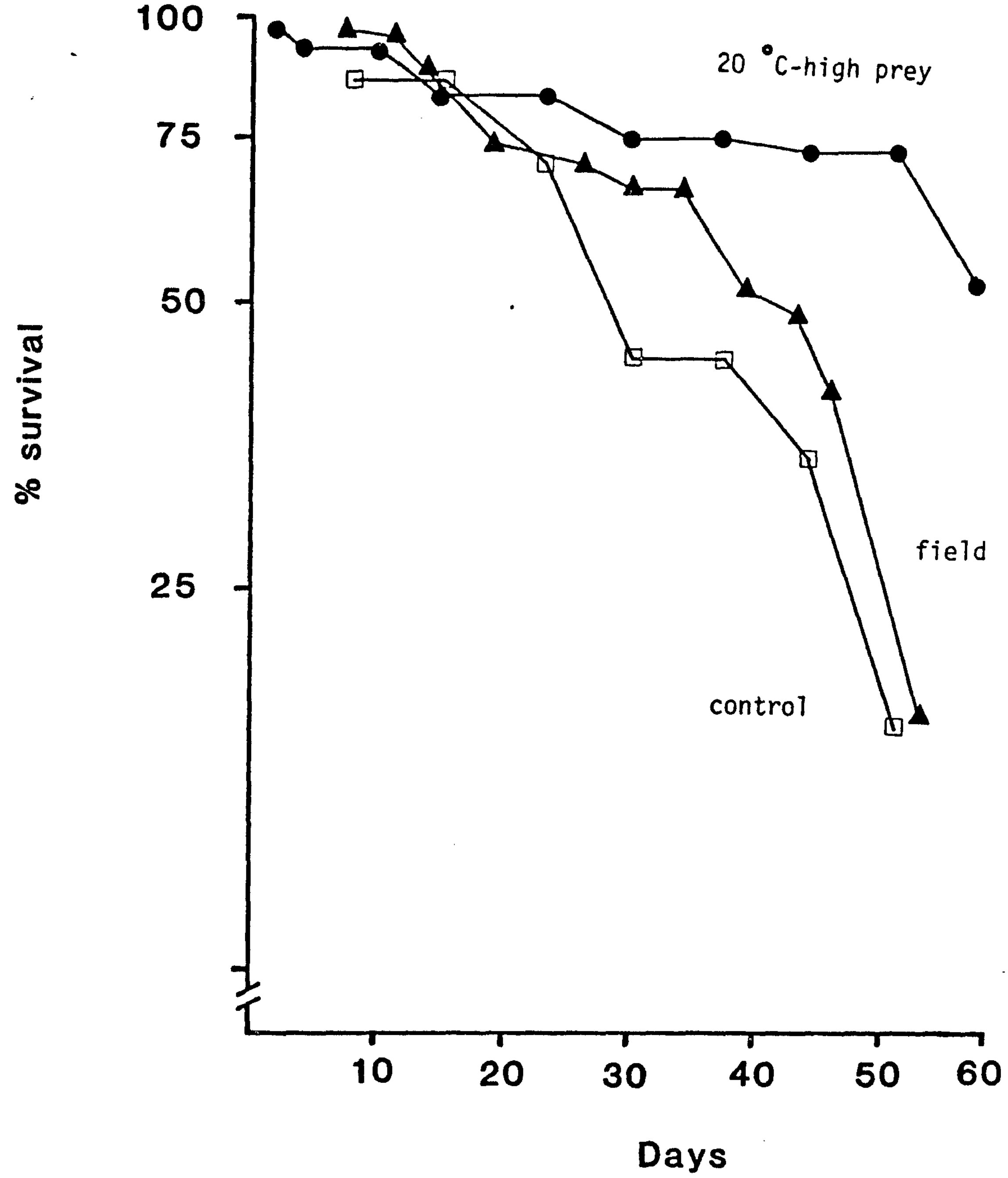

Figure 21. Survival of Lestes disjunctus disjunctus nymphs from the field population, the control competition-predation pool, and the 20°C high prey density treatment.

To test the accuracy of the prey specific growth model growth of nymphs in the field was predicted using field temperature data and compared with growth observed in the field. Predicted growth approximates observed growth in the field through day 36 and begins to diverge at day 43 (Figure 22). Growth in the field between day 43 and 51 was much greater than predicted (Figure 22). However, water temperatures in the field were also greater than the highest treatment temperature during this period.

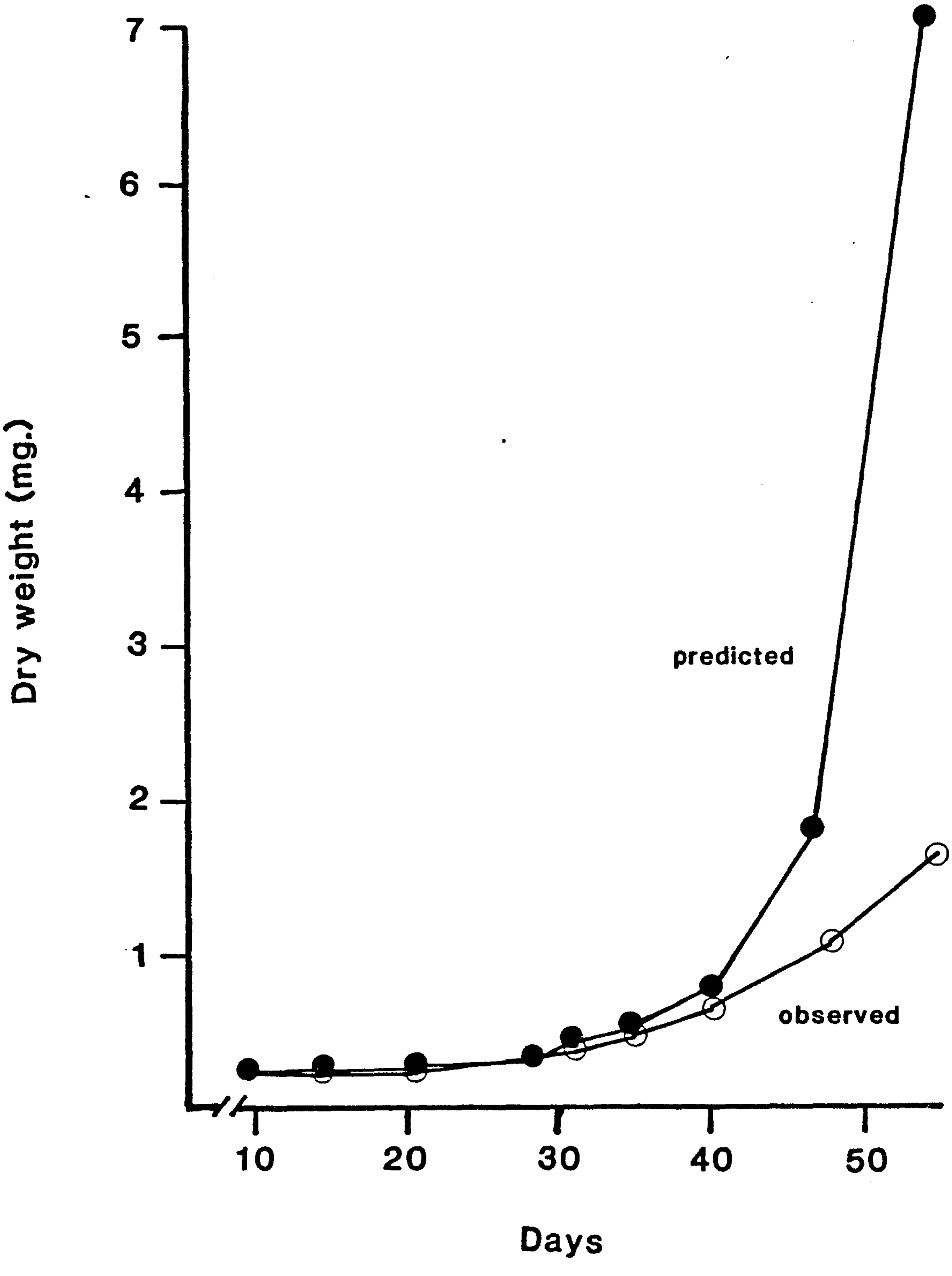

Figure 22. Comparison of Lestes disjunctus disjunctus nymphal growth in the field with predicted growth.

DISCUSSION

Water Temperature-Prey Density

Nymphal growth in *L. d. disjunctus* was significantly influenced by water temperature but not prey density in the water temperature-prey density experiments. Under natural conditions, water temperature may influence nymphal growth by influencing both prey turnover rates (Hall 1964; Threlkeld 1980) and predator functional response (Cresens et al. 1982), as well as the bioenergetics of nymphs. Thus a clear distinction between temperature and prey density effects is tenuous. Temperature also influences food assimilation and food conversion efficiency, enzyme kinetics, and endocrine processes (Vannote and Sweeney 1980; Sweeney and Vannote 1981). For example, respiration in *L. d. disjunctus* nymphs fluctuates on a diel basis in response to diel changes in water temperature and dissolved oxygen tension (Erickson 1984).

Growth of nymphs predicted from the prey density specific growth model closely approximated observed growth in the field until field water temperature increased above the highest test temperature. Since the greatest proportion of growth took place during this period of warmer water temperature it is not certain the model would accurately predict growth in the field even though predictability is quite good at lower water temperatures.

A positive relationship between increasing water temperature and growth rates of aquatic insects from natural populations has been demonstrated numerous times (Mackay 1979; Johannsson 1980; Merrit et al. 1982). Controlled experiments have also shown that growth rates of aquatic insects generally increase with increasing water temperature (Heiman and Knight 1975; Sweeney 1978; Ward and Cummins 1979). However, for cold adapted species increased growth is often correlated with decreasing water temperature (Grafius and Anderson 1979).

While controlled experiments are of value in elucidating mechanisms such as the relationship between temperature and growth the use of constant temperatures has been criticized as not refelecting the heterogeneous thermal environment of many aquatic insects (Vannote and Sweeney 1980). These authors argue that diel thermal fluctuations may significantly influence the growth and development of aquatic insects (Vannote and Sweeney 1980; Sweeney 1984). Similar developmental rates from constant and fluctuating water temperature experiments have been reported, though (Humpesch 1982).

The influence of food quantity and quality on development of aquatic insects is neither as well documented nor understood as the effects of temperature. Results from the present study indicate that prey density significantly influenced survival of nymphs of L.d. disjunctus while water temperature did not. These results were somewhat surprising as previous studies of Zygoptera suggest nymphs can survive long periods without food and that a very narrow range of prey densities may separate 0 and 100% survival (Lawton et al. 1980). Other investigators have suggested food quantity or prey abundance is rarely limiting under natural conditions (Benke 1978; Vannote and Sweeney 1980; Vodopich and Cowell 1984).

Under experimental conditions, food quality has been shown to be limiting to growth and development of the chironomid larvae Paratendipes albimanus however (Ward and Cummins 1979). Ward and Cummins (1979) produced two generations of this chironomid per year from a population normally univoltine in Augusta Creek, Michigan by providing high quality food in summer when food present in the creek is of low quality. Variation in food quality among microcrustacean prey commonly consumed by L. d. disjunctus nymphs and many other predaceous aquatic insects does not appear to be great enough to significantly influence growth and development (Cummins and Wychuck 1971; Vijverberg and Frank 1976). The greater mortality observed at low prey treatments in the present study may have resulted from cannibalism (Gallepp 1974).

Competition-Predation

Nymphs of L. d. disjunctus in competition-predation experiments experienced significantly greater mortality in the presence of A. canadensis nymphs than they did in either the control or other treatment pools. None of the other comparisons of mortality or growth among pools was significant. However, several patterns did emerge from the data which, while not statistically significant, are suggestive. First, initial high mortality in the E. hageni pool combined with results from the A. canadensis pool suggests that these larger odonates may prey on the smaller L. d. disjunctus nymphs. Second, growth of L. d. disjunctus was inversely proportional to survival indicating intraspecific competition for food resources may influence growth.

Comparison of nymphal survival among the field population, the control pool, and 20°C high prey treatment micrococosom also suggest intraspecific competition, as survival in the control pool was nearly identical to that in the field. Survival in both the control pool and the field were roughly 30% lower than in the 20°C high prey treatment during a comparable time period and roughly 20% lower than when the temperature experiments were terminated. This 20 to 30% difference may reflect the magnitude of intraspecific interaction on survival.

Dietary analysis have been conducted for four of the five dominant odonates inhabiting the study site in the littoral zone of the St. Marys River. These studies lend support to the hypothesis of inter-odonate predation regulating odonate populations as well as influencing survival in the competition pools. Zygoptera comprised 1.7% of the diet of *A. canadensis* during spring when *L. d. disjunctus* populations consist of early instar individuals most vulnerable to predation (Day 1983). However, odonates were not found in the diet of the anisopteran *Libelulla* spp. nor in the diet of the zygopterans *Enallagma boreale* or *L. d. disjunctus* (Day 1983; Duffy unpublished). Low rates of cannibalism (Fox 1975) or inter-odonate predation have been shown to influence survival in natural populations (Benke 1978). Benke (1978) estimated that consumption of one odonate per day by only 6.8% of the larger odonates in a South Carolina pond would be sufficient to account for the mortality observed for smaller species. He suggested inter-odonate predation was an extreme form of interference competition.

More recent studies of a diverse odonate community inhabiting a Tennessee lake have addressed species interactions and competition. Field studies over a three year period indicated interspecific competition was of little importance in obtaining food resources (Crowley and Johnson 1982). Rather, Crowley and Johnson (1982) believed habitat determined interactions and seasonal segregation acted to reduce interactions. Enclosure experiments with both damselflies and dragonflies from this same community have also failed to demonstrate exploitation (resource) competition (Johnson et al. 1985). However, these authors have suggested interference competition in the form of inter-odonate predation as a mechanism regulating populations of the dominant species in this community.

The contention that growth is influenced by intra-specific interactions is based on the observed inverse relationship between growth and survival. Intra-specific interactions were also suggested as more important in inhibiting access to food resources than inter-specific interactions by Crowley and Johnson (1982). The probability of nymphs locating and remaining in a favorable feeding site should be inversely related to population density. In a series of behavioral experiments, Baker (1980, 1981a,b) has demonstrated that nymphs of *Coenagrion resolutum* and *L. disjunctus* locate and defend favorable feeding sites. Success in defending a feeding site is apparently related to size. In populations of similar sized nymphs smaller individuals were capable of repulsing slightly larger individuals, however, small nymphs could not defend feeding sites from much larger nymphs (Baker 1980, 1981a).

Both mortality and growth are ultimately reflected in fitness. For most aquatic insects, fecundity is linearly related to female size (Sweeney and Vannote 1981; Sweeney 1984). Furthermore, net reproductive effort is the product of survival and young produced and for semelparous species such as insects is a measure of fitness (Mitchell 1981). This relationship of mortality and growth has apparently not been quantified in aquatic insects but has been for bluegill by Werner and his colleagues who illustrate how decreased growth can equal higher mortality (Werner et al. 1983).

Habitat Selection

Bluegill sunfish clearly influence both the distribution and survival of L. d. disjunctus nymphs under experimental conditions. In the absence of fish, nymphs were relatively uniformly distributed both among and within (on macrophytes, sediments, and aquaria sides) the three cover densities. Following the introduction of bluegills, surviving nymphs either selected or were restricted to macrophytes. These results are in general agreement with previous investigations of fish-invertebrate interactions reported for littoral zones which suggest fish exert a major influence on invertebrates in this habitat (Hall et al. 1970; Crowder and Cooper 1982). These laboratory results also corroborate field studies which found L. d. disjunctus nymphs restricted to dense cover provided by Sparganium eurycarpum.

The importance of aquatic macrophytes in providing refugia for larger littoral zone invertebrates is becoming increasingly better documented. Macan (1977) provides several examples from a long term study of Hodson's Tarn. One species in the tarn, Lestes sponsa, disperses from hatching sites to Myriophyllum spp. much like L. d. disjunctus in the St. Marys River moves to S. eurycarpum. Following the introduction of brown trout (Salmo trutta) to this tarn L. sponsa dissappeared, returning only after most of the fish had been removed. Two other species of Coenagrionidae declined in density following the introduction of brown trout, then were drastically reduced in number when macrophyte cover was lost (Macan 1977). Changes in vegetation density and the presence or absence of fish often result in shifts, not only in odonate density or species composition, but in the entire invertebrate community (Crowder and Cooper 1982; Morin 1984; Gilinsky 1984).

This study consisted of several experiments intended to describe mechanisms influencing growth, survival, and habitat selection of L. d. disjunctus in the St. Marys River. Results from this and other studies emphasize the importance of lentic littoral zones as valuable habitats for invertebrates as well as fishes. Littoral zones have a more heterogeneous diel and annual thermal regime which favors the growth and development of a wider array of species (Ward and Stanford 1982; Sweeney 1984). Littoral zone habitats are also more physically complex and patchy than either profundal or limnetic zones. This increased structural complexity creates a greater amount of microhabitat types (Crowder and Cooper 1982) and reduces predator efficiency thereby stabilizing predator-prey interactions (Crowley 1978; Anderson 1984; Cook and Stearns 1984).

CONCLUSIONS

Quantitative aspects of the life histories of many aquatic insects are lacking or available for only portions of life cycles. In this study age specific life table techniques were used to investigate the demographics of a natural population of Lestes disjunctus disjunctus. Laboratory studies of mechanisms influencing population biology were integrated with the field investigation.

Both absolute mortality (d_x) and relative mortality (q_x) were found to be greatest in the egg stage. The greatest single identifiable source of mortality in eggs was related to vegetation loss resulting from Lake Superior level management and commercial navigation which influenced river water level and current patterns. However, egg mortality from overwintering was nearly as high. Mortality from vegetation loss was sufficient to reduce the population rate of increase from roughly neutral or zero growth to -0.612. Population adjustments to vegetation loss, either physiological or behavioral, are improbable because of the highly irregular nature of this event. Other sources of mortality to both the egg and nymphal stages, while of a magnitude to potentially regulate population growth, occur with greater regularity and are more likely offset through physiological or behavioral population adjustments.

Laboratory studies provided insight into the mechanisms regulating natural populations of *L. d. disjunctus*. Water temperature and prey density clearly influence growth and survival. However, interactions among water temperature and prey (food) levels make separation of the influence each has on growth or survival problematic. Laboratory studies also demonstrated that invertebrate and vertebrate predators (bluegill) influence both survival and habitat selection by nymphs.

SUMMARY

The population ecology of Lestes disjunctus disjunctus, a common zygopteran of ponds and lake margins in north temperate North America, was investigated during 1982 and 1983 using integrated field and laboratory studies. Field studies were carried out in the Lake Nicolet basin of the St. Marys River, Michigan. Laboratory studies were conducted to examine the influence of water temperature, prey density, and coexisting predators on growth and survival of nymphs. Additional laboratory studies examined the influence of fish on survival of and habitat selection by nymphs.

The St. Marys River is the single outflow from Lake Superior. Average monthly discharge during the period of study ranged from 1,229 - 2,979 m^3/sec. The Lake Nicolet basin receives about 65% of this flow and water retention time within the basin is short (< 24 hr) promoting high water quality during all seasons. Along protected shorelines extensive emergent wetlands are present, characterized by well developed beds of Scirpus acutus and Sparganium eurycarpum. The study site was located within one such emergent littoral zone on the west shore of Lake Nicolet.

In the St. Marys River L. d. disjunctus oviposits exclusively in green stems/leaves of S. eurycarpum during July and August. The average number of eggs oviposited per female was estimated to be 73.5 in 1982 and 45.2 in 1983. Eggs oviposited in summer apparently entered diapause in autumn with termination of diapause in spring being temperature and possibly moisture related. Eggs collected in September and refrigerated successfully hatched while eggs not refrigerated failed to hatch. Egg hatching rate was positively related to water temperature and could be described by the regression equation:

$$\% \text{ hatching/day} = -1.63 + 0.38(T),\ r^2 = 0.95.$$

The threshold temperature was determined to be 4.3°C.

Nymphs were first collected on 14 May in 1983. Development through 10 nymphal instars was rapid averaging 18.5 days/instar. Emergence began on 10 July, 1983, 58 days following the appearance of first instar nymphs. Nymphs were restricted in distribution to areas of dense cover, which consisted of either mats of dead vegetation or S. eurycarpum. Maximum density of nymphs$\cdot m^{-2}$ was 105.8.

Adults emerged from the St. Marys River in early July. Densities of adults emerging from heavy and medium density beds of S. eurycarpum averaged 2.1 and $0.9 \cdot m^{-2}$ respectively. The tenneral period following hatching was spent along the tree line 100-200 m in from the waters edge. After this period the still sexually immature adults returned to the emergent wetland. Average life of adults was 6.0 days.

Estimated population sizes of selected stages in the 4.03 ha study area were as follows: eggs 3,202,000; instar I 730,800; instar X 128,500; and adults 35,800. Mortality in the egg stage was partitioned into that occuring from loss of vegetation, overwintering, hatching difficulty, and unexplained. Overall survival from egg to adult female was 1.2%.

The net reproductive effort for L. d. disjunctus in the study area was 0.542. Population rate of increase between 1982 and 1983 was -0.612. Mortality in the egg stage attributed to vegetation loss, a stochastic event, was great enough to explain the negative rate of population increase.

In the laboratory, nymphs in 20°C treatments achieved significantly greater growth than nymphs in 16°C treatments. Prey density did not significantly influence growth of nymphs nor did the presence of coexisting predators. Maximum prey specific growth rates at 16 and 20°C were 0.39 and 0.70 percent per day respectively. Growth predicted from specific growth rates approximated that of nymphs in the field through day 36, thereafter underestimating growth in the field. Failure to accurately predict growth in later stages may have been related to warmer water temperatures in the field.

Survival of nymphs was significantly influenced by prey density but was not significantly influenced by water temperature. Survival was also significantly lower in the presence of another odonate, Aeshna canadensis, than in the presence of other coexisting predators or a control. Survival of nymphs in the field and control pool from competition-predation experiments were similar and 20 - 30% lower than in 20°C - high prey density treatments. This difference is potentially the influence of intraspecific interactions.

APPENDIX

Table 18. Density of macroinvertebrates as mean number over 1 m^2 of substrate in *Sparganium eurycarpum* beds located in a littoral zone of the St. Marys River.

	Date										
Taxa	4-19	5-5	5-13	5-21	5-27	6-3	6-9	6-17	6-22	6-29	7-6
COELENTERATA											
Hydrazoa											
Hydroida											
Hydra americana						64	128	117	14		
PLATYHELMINTHES											
Turbellaria											
Tricladida											
Dugesia spp.						16	64	53		35	336
ANNELIDA											
Oligocheata											
Haplotaxida											
Naididae											
Stylaria fossularis		333	256	576	752	3504	1456	3912	5670	4361	2485
Vejdovskyella comata						576	128	259	14	455	343
Nais communis						96	48		21	28	301
N. barbata						144		63			
N. simplex							48	53	105	63	280
Pristina longiseta longiseta						32			7	7	728
Chaetogaster limnae						160	352	555	1153	371	154
Stevensoniana trivandana									21		
Tubificidae											
Peloscolex ferox									14	196	

Table 18. (cont'd.).

Taxa	Date 4-19	5-5	5-13	5-21	5-27	6-3	6-9	6-17	6-22	6-29	7-6
Hirudinea											
Rhynchobdellidae											
Glossiphoniidae											
Batracobdella michiganiensis								11			
Glossophonia complanata			8								
Helobdella fusca										7	
H. michiganiensis						16		256		7	
H. stagnalis							32	21	35	7	441
Pharyngobdellidae											
Erpobdellidae											
Erpobdella punctata								11			
ARTHROPODA											
Crustacea											
Isopoda											
Asellidae											
Asellus intermedia				16		432	928	270	196	21	14
Amphipoda											
Talitridae											
Hyalella azteca			80	32	336	64	32	300	427	119	357
ARACHNIDA											
Acarina											
Hydracarina			32	256	208	320	176	230	147	28	271

Table 18. (cont'd.).

Taxa	Date 4-19	5-5	5-13	5-21	5-27	6-3	6-9	6-17	6-22	6-29	7-6
Insecta											
Collembola			24	16	160				14		
Ephemeroptera											
Baetidae											
Callibaetis spp.								7	7		
Cloen spp.											7
Baetiscidae											
Baetisca spp.										14	
Caenidae											
Caenis spp.			8	16		800	544	725	168	392	343
Odonata											
Zygoptera											
Coenagrionidae											
Enallagma boreale		48	56	53	64	16				7	630
E. hageni		8	32	11	16	28		33	16	7	
Lestidae											
Lestes disjunctus disjunctus			13	106	95	81	47	51	30	17	7
Anisoptera											
Aeshnidae											
Aeshna canadensis				11		16	28	18	14	11	
Libellulidae											
Libelulla spp.						16		14	18		
Sympetrum rubicundilum										7	

Table 18. (cont'd.).

Taxa	4-19	5-5	5-13	5-21	5-27	6-3	6-9	6-17	6-22	6-29	7-6
Hemiptera											
Corixidae											
Sigara alternata			8					21	28	35	7
Notonectidae											
Buenoa spp.					16	16	32	7	21		14
Hebridae											
Hebrus spp.								7			
Merragata spp.								21			
Mesoveliidae											
Mesovelia spp.								268	140	112	28
Veliidae											
Microvelia spp.							7		7		
Trichoptera											
Hydroptilidae											
Ochrotrichia spp.		84									
Oxyethira spp.									7	21	77
Leptoceridae											
Ceraclea spp.		125				48	16	200	77	21	84
Mystacides spp.											
Oecetis spp.											
Trianodes spp.		84				96	112	75	7	14	28
Limnephilidae											
Grammotaulus spp.			127	32	48	192	32	7	14		14
Nemotaulus spp.							16				
Phryganeidae											
Phryganea spp.								32			7
Polycentropodidae											
Polycentropus spp.							16	99	35	63	
Lepidoptera											
Acentropus spp.						16			7		

Table 18. (cont'd.).

Taxa	Date										
	4-19	5-5	5-13	5-21	5-27	6-3	6-9	6-17	6-22	6-29	7-6
Coleoptera											
Chrysomelida (adult)					16						
Donacia spp.								119	91	84	77
Dytiscidae											
Hydrovatus spp.									21		
Haliplidae											
Haliplus spp. (larvae)						16	11				
(adult)						16		11			
Hymenoptera										7	
Diptera											
Ceratopogonidae											
Alludomyia needhami					368	384	341		84		
Bezzia varicolor		125	48		128	48	64	32	133	42	1295
Culicoides spp.					32		21	7			
Palpomyia prunescens						32					
Chironomidae											
Ablabesmia spp.			16	16	96	320					
Labrundinia spp.						32	80		107	833	35
Larsia spp.		333	704	240	160	720	480	371	315	134	777
Dicrotendipes spp.		125			48	96	16		126		1463
Endochironomus spp.			8				384				504
Enfeldia spp.			48								
Glyptotendipes spp.								21			
Lauterborniellia spp.						48	240			35	280
Microtendipes spp.						208	176	7		63	
Parachironomus spp					48				56		
Paratanytarsus spp.			120	48	16	208	96	7	77	21	
Polypedilum spp.	178		80	96		384	464	43	7	539	11312

Table 18. (cont'd.).

Taxa	4-19	5-5	5-13	5-21	5-27	6-3	6-9	6-17	6-22	6-29	7-6
Chironomidae (cont'd.)											
Phaenospectra spp.							64		7		
Psectrocladius spp.		125	320	32				1000	1414	666	672
Pseudochironomus spp.							288			21	
Stichtochironomus spp.							32				
Tanytarsus spp.							64	35	112	21	
Corynoneura spp.	357			144	64	592	16	77	406	28	231
Cricotopus spp.	178	84	144	64				35			
Heterotrissocladius spp.						32					
Orthocladius spp.										21	
Culicidae											
Aedes intrudens							16	7			
Dixidae											
Dixa spp.						32					
Empididae								7			
Sciomyzidae											
Sepedon fuscipenis						16					
Stratiomyidae											
Stratiomys spp.								11			
Tipulidae											
Erioptera spp.							16				

Table 18. (completed).

Taxa	Date 4-19	5-5	5-13	5-21	5-27	6-3	6-9	6-17	6-22	6-29	7-6
MOLLUSCA											
Gastropoda											
Basommatophora											
Ancylidae											
Ferrisia paralella											7
Lymnaeidae											
Pseudosuccinus columella				48	16	80		7		14	
Physidae											
Physa gyrina gyrina			8	16				11	70	105	98
P. integra								242			
P. jennessi skinneri				16							
Planorbidae											
Helisoma anceps anceps			8								
H. corpulentum vermilion								14	7	35	14
Gyraulus parvus				16	16	128	16	11		14	
G. deflectus			64					7	14	14	175
Promenetus exacuous exacuous						16	32	25	14		7
Planorbula armiger							16				
Pelecypoda											
Eulamellibranchia											
Sphaeriidae											
Sphaerium securis			16		16	16		42	35	21	182
TOTAL	713	1418	2135	1680	2160	10080	7104	10245	12108	8402	24043

Table 19. Annual production estimates for <u>Lestes disjunctus disjunctus</u> from the St. St. Marys River.

	Shore Habitat					*Sparganium eurycarpum*				
Date	N (no/m²)	ΔN	W (mg)	$\bar{W}$	$\bar{W}$(ΔN)	N (no/m²)	ΔN	W (mg)	$\bar{W}$	$\bar{W}$(ΔN)
May 14	12.8		0.19							
		-74.6		0.19	-14.55					
17	87.4		0.20							
		-18.4		0.21	-3.77					
20	105.8		0.21							
		0.4		0.21	0.08					
24	105.4		0.21							
		10.3		0.21	2.16					
27	95.1		0.21							
		14.5		0.23	3.26					
June 2	80.6		0.24							
		3.4		0.26	0.88					
9	77.2		0.28							
		5.2		0.35	1.79					
13	72.0		0.41							
		-5.1		0.46	-2.35					
17	77.1		0.51			15.5		0.51		
		39.7		0.63	24.81		-5.2		0.63	-3.25
22	37.4		0.74			20.7		0.74		
		25.4		1.09	27.69		-1.6		1.34	-2.14
29	12.0		1.43			22.3		1.93		
		6.8		2.74	18.63		13.6		5.51	74.94
July 6	5.2		4.05			8.7		9.09		
		0		5.75	0		8.7		9.97	86.74
13	5.2		7.44			0.1		10.84		

Total annual production (mg/m²) = 58.63 = 156.29
Weighted mean annual production = 134.72 mg/m²

Table 20. Production statistics for common macroinvertebrates of *Sparganium eurycarpum* beds in the St. Marys River, Michigan.

Taxon	$\bar{N}$ (no/m^2)	$\bar{B}$ (mg/m^2)	Uncorrected P (mg/m^2)	$\frac{DT}{CPI}$	Annual P (mg/m^2)	Annual P/B
Ephemeroptera						
Caenis spp.	273	71.3	50.5	6	303.2	4.25
Trichoptera						
Ceraclea spp.	57	11.3	5.7	5	28.5	2.52
Trianodes spp.	4	8.8	6.3	6	37.8	4.28
Polycentropus spp.	25	29.9	16.2	5	80.8	2.70
Grammotaulus spp.	46	81.3	33.5	6	201.0	2.47
Chironomidae						
Larsia spp.	370	32.0	32.9	5	164.5	5.14
Paratanytarsus spp.	141	2.7	2.1	3	6.3	2.33
Polypedilum spp.	1187	216.5	176.0	5	879.9	4.06
Psectrocladius spp.	328	53.8	38.8	4	155.4	2.89
Amphipoda						
Hyalella azteca	1059	756.9	749.8	3	2249.7	2.97
Isopoda						
Asellus intermedia	187	76.3	76.4	5	381.9	5.01
Oligocheata						
Stylaria fossularis	2004	523.0	340.8	6	2044.7	3.91

Table 21. Total number of prey in guts of *Lestes disjunctus disjunctus* collected from *Sparganium eurycarpum* beds in the St. Marys River, Michigan.

Taxon	May			June				July	Sub Total
	13	21	27	3	9	22	29	6	
CLADOCERA									
Acroperus spp.			1	3	2	21	15	22	64
Alona spp.						5	1		6
Bosmina spp.							5	6	11
Camptocercus spp.				1	1	7	1		10
Chydorus spp.		2	2	10	13	74	121	39	261
Chydoridae		1	5	1	7	21	50	8	93
Eurycercus spp.					1	4	9	6	20
Graptoleberis spp.						2			2
Macrothrix spp.					1				1
Pleuroxus spp.							1	3	4
Polyphemus spp.							2		2
Sida spp.						6	7	2	15
Simocephalus spp.					2	1			3
Unidentified Cladocera				2	2	1			5
COPEPODA									
Macrocyclops spp.						3	2	1	6
Cyclopoida copepodids	2	7	16	12	16	39	9	9	110
Harpactacoida				1	4	1	1	1	8
Copepoda nauplia	3	4	5						12
ROTIFERA									
Keratella spp.			4		2		1		7
OSTRACODA				1			2	3	6
CHIRONOMIDAE									
Corynoneura spp.				1		3		1	5
Dicrotendipes spp.						1			1
Labrundinia spp.						2			2
Larsia spp.							2		2
Polypedilum spp.								1	1
Pseudochironomus spp.								1	1
Tanytarsus spp.							14	3	17
Unidentified Chironomidae	1			1			3		5
Total Prey	6	14	33	33	51	191	246	106	680
Total Nymphs	7	11	18	15	15	14	15	9	104
Ave. Prey/Gut	0.9	1.3	1.8	2.2	3.4	13.6	16.4	11.7	6.5

Table 22. Density of zooplankton as mean number/liter in *Sparganium eurycarpum* beds located in a littoral zone of the St. Marys River.

	Date										
Taxa	4-19	5-5	5-13	5-21	5-27	6-3	6-9	6-17	6-22	6-29	7-6
ARTHROPODA											
Crustacea											
Cladocera											
Acroperus harpae		1	3	17	24	34	70	33	65	45	74
Alona guttata				4		20	38		11	19	
A. exigua								5			
A. intermidia										11	
A. quadrangularis									4		25
A. rectangularis				4	7		15	2	38		21
Alonella acutirostris									16		30
Bosmina longirostris							1	1			11
Camptocerus rectirostris					2		5	3	24	18	12
Ceriodaphnia megalops			1								
C. quadrangula						40					1
Chydorus gibbosus										3	
C. sphaericus	3	1	77	43	114	285	90	98	114	98	122
Daphnia spp.							1				
Eurycercus lamellatus			1	2		1	13	4	18	53	14
Graptoleberis testudinella			7		2	7			11	3	6
Ilyocryptus spinifer						1					
Lathonura rectirostris			7								
Macrothrix rosea						7	33	14	88		
Ophryoxus gracilis				16						3	6
Pleuroxus denticulatus			2					7		21	2
P. procurvus		1	3			33		1			
P. truncatum				2							
P. uncinatus							7				
Polyphemus pediculus										3	
Sida crystallina				1	7			7	7	22	
Simocephalus serrulatus				16		53	16	14	56	20	47

Table 22. (completed).

	Date										
Taxa	4-19	5-5	5-13	5-21	5-27	6-3	6-9	6-17	6-22	6-29	7-6
Copepoda											
Macrocyclops albidis				3	1	27	66	9	11	10	10
Cyclopoida copepodida		1	27	16	1	53	81	44	100	51	46
Cyclopoida nauplia			24	5		40	30	20	28	5	1
Harpactacoida		1	7			7	12	4	11	7	6
Ostracoda		1	2	1	34	66	25	2	19	17	34
Total	3	5	159	128	191	672	502	266	620	406	468

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